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A Projection of the Recreational Use of Public Forest Areas in California to 1965

BY
JOHN ZIVNUSKA
ANN SHIDELER

RECREATION has long been recognized as an important use of the forest resources of the United States. Under the impact of rapid increases in recreational visits to forest areas combined with anticipations of a continuing expansion of population and increases in general economic well-being, there is ample reason for intensified interest in the future levels of this form of use of the forests. This interest is a part of a general concern with the availability and use of natural recreational resources in the nation which is manifesting itself in various proposals for a comprehensive, nation-wide study in this field. Titles such as "Scenic Resources Review" have been suggested to indicate a scope of coverage comparable to that of the Timber Resource Review recently conducted by the U. S. Forest Service, and bills have been introduced in The Congress to provide for such a study.

Whether or not a national study is undertaken in the next few years, there is need for formulation of the specific questions to be answered by such an inquiry, for the development of appropriate models for analyzing these questions, and for review of the availability and suitability of data for testing and quantifying these models. The 50-year record of difficulties due to changing standards and concepts in timber reviews should be adequate evidence of the importance of the most thorough analysis of the problems prior to undertaking national resource studies.

During such a period of preliminary analysis a series of localized studies of restricted scope can be helpful in focusing on various aspects of the problem. The analysis presented here is intended as one such localized and exploratory study. Developed in California, the setting is that of a region in which the character of the forest, the type of climate, and the urbanized and rapidly expanding population combine to make recreational use of the forest exceptionally heavy and of substantial economic importance. Thus it is hoped that the study will also have some interest and value in its own right.

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The study is designed to answer a single question. Assuming no major changes in the conditions which have surrounded forest recreation in the last 10 years in California but allowing for a continuation of the past trends in these conditions, what will be the level of recreational use of the public forest areas by 1965?

The Statistical Analysis

The statistical basis of this study directly parallels the techniques which have been used in various projections of future consumption of forest products (Stanford Research Institute, 1954; Vaux, 1950) as well as in many other economic analyses. It involves the determination of the past relationship of the variable under study to one or more independent variables through the methods of correlation analysis, followed by projection of the dependent variable into the future on the basis of the anticipated magnitudes of the independent variables. To be useful for this purpose, the relationship developed must meet at least four important conditions:

1. The relationship postulated must be based on sound theoretical reasoning.
2. Quantitative expressions of the variables must be available for a period of record.
3. It must be possible to project the independent variables into the future more readily than the dependent variable.
4. There must be a significant correlation between the dependent variable and the independent variables during the period of record.

Data on recreational use were obtained from the San Francisco offices of the National Park Service and the U. S. Forest Service. The Park Service data included records of the number of visitors from 1936 through 1955 and the number of visitor-days from 1944 through 1955 for Yosemite National Park, Sequoia and Kings Canyon National Parks, and Lassen Volcanic National Park. The Forest Service data included the number of visitor-days in various categories of recreational use for the National Forests of California[1] for the period 1941 through 1955. In the analysis the period 1942 through 1945 was dropped due to the effects of World War II.

The next step was to determine the type of statistical relationship to be used in developing the projections of future use. A number of hypotheses were considered, of which the following three examples are illustrative: (a) recreational use is associated with the size of California population; (b) recreational use is associated with the size of California population and with individual income levels as indicated by gross national product on a per capita basis; and (c) recreational use is associated with the size of California population, gross national product on a per capita basis, and other factors which can be lumped as trend.

These hypotheses were tested first with the Park Service records of total visitor-days for all the National Parks in California for the period 1946-55. The relationship of these visitor days to California population, gross national product on a per capita basis, and trend gave an adjusted multiple correlation coefficient of 0.98, but due to the high intercorrelation of the independent variables only trend had a regression coefficient significantly different from zero at a 5 percent level of significance or better. The relationship of these visitor days to California population and gross national product on a per capita basis gave an adjusted multiple correlation coefficient of 0.97 with the regression coefficient for population being significant at the 0.25 percent level of significance. Again the coefficient for gross national product per

[1]Data used are for Region Five of the Forest Service, which covers California primarily but includes minor areas in Oregon and Nevada and excludes some National Forest areas in eastern California which are in Region Four.

capita was not significantly different from zero. The relationship of visitor days to California population alone on a linear basis also yielded a correlation coefficient of 0.97 with a significant regression coefficient for population.

Similar tests of relationship were made for several other series. In all cases the results were comparable to those reported above. On the basis of the statistical tests it would appear that either trend or the size of California population might be used as the independent variable. However, there is a logical causal relationship between population size and recreational use which does not appear to exist between trend and recreational use. Although it is possible that some variable in addition to population might be found that would show a significant relationship, it is apparent from the very high correlation coefficients for the relationship to California population alone that the addition of any such variable could not be expected to improve the fit very much.

It should be noted that these statistical results do not in any way disprove the common contention that the intensity of recreational use is influenced by income levels, length of vacation periods, methods of transportation, and so on. Actually, the data analyzed are not satisfactory for investigating these possibilities statistically due to the fact that all of these factors tended to vary with size of population during this period. Thus it is possible that they are appropriate variables for the recreational use relationship even though this is not statistically demonstrable in the data analyzed. This situation involves a real danger that the statistical relationship between recreational use and California population might not hold during a period in which these other factors did not happen to vary with population.

On the basis of the foregoing analysis it was decided to use the linear relationships of each of the recreational use series to California population as the basis for developing the desired projections of future use. In Table 1 there is presented a summary of the estimating equations which were developed, together with their standard errors of estimate and coefficients of determination (which measure the proportion of the variance of each of the types of recreational use which is associated with California population through the equations developed).

For the National Park data the fit of the equations is excellent, with nearly all of the variance in reported use being associated with California population. A possible exception is the estimating equation of visitor-days at Yosemite which has a noticeably lower coefficient of determination than the other Park series, but even here the degree of association is high.

The equations for visitor days at Forest Service campgrounds and picnic areas also fit the data very closely. With the other Forest Service series, however, various special problems were encountered.

In the case of organization camps the reported use for 1946 is entirely out of line with the following years. This was due to the very heavy use of an Armed Forces rest camp established during World War II and not discontinued until the end of 1946. Accordingly this year was dropped from the series and an excellent fit was obtained for the period 1947-1955.

The very high reported use of recreational residences for 1951 appears to have been due to a reporting error, with one forest including use of residences constructed for recreational use but subsequently changed to year-round use. Similarly the 1948 report of winter sports use was greatly affected by the report of one forest which included the use of several winter sports areas on private land within the forest boundary. Again in the case of wilderness use the 1953 report is totally out of line with the other years, although the reason for this has not been determined. In each of these cases the questionable year was dropped and a good fit obtained to the

TABLE 1. The estimating equations.

Period used in deriving equation	Area of recreational use	Relationship of recreational use to California population[1]	Standard error of estimate	Coefficient of determination
The National Parks in California:				
1946-55	Yosemite	$X'_1 = 0.097X_2 - 213$	43.7	.89
		$X''_1 = 0.168X_2 + 503$	110.0	.79
1946-55	Kings Canyon and Sequoia	$X'_1 = 0.154X_2 - 900$	44.3	.95
		$X''_1 = 0.213X_2 - 1160$	44.6	.97
1946-55	Lassen Volcanic	$X'_1 = 0.050X_2 - 352$	15.9	.94
		$X''_1 = 0.064X_2 - 443$	19.2	.95
1946-55	Total	$X'_1 = 0.300X_2 - 1468$	75.2	.96
		$X''_1 = 0.446X_2 - 1110$	138.4	.94
The National Forests in California:				
1946-55	Campgrounds	$X''_1 = 0.653X_2 - 2560$	346.4	.85
1946-55	Picnic areas	$X''_1 = 0.148X_2 - 1128$	48.2	.94
1946-47, 1949-55	Winter sports areas	$X''_1 = 0.231X_2 - 1951$	145.9	.90
1947-55	Organization camps	$X''_1 = 0.141X_2 - 444$	48.4	.93
1950-55	Hotels and resorts	$X''_1 = 0.135X_2 - 942$	36.4	.97
1946-50, 1952-55	Recreational residences	$X''_1 = 0.357X_2 - 1740$	207.9	.84
1946-52, 1954-55	Wilderness areas	$X''_1 = 0.080X_2 - 595$	43.5	.92
1949-55	Other forest areas	$X''_1 = 0.751X_2 - 6440$	215.1	.97

[1]In the equations, X'_1 = thousands of visitors, X''_1 = thousands of visitor days, and X_2 = California population in thousands.

data for the remaining nine years.

The series on use of hotels and resorts on Forest Service land involves a very different situation. In view of the source of the data, the reported use data should be reliable. Due to various special circumstances the use of such facilities appears to have built up to a very high level by the end of World War II and then to have remained at a high level somewhat below this peak through 1948. Due to what amounted to a basic change in the conditions surrounding such use, there was then a precipitous drop to the 1950 level; since that time the trend has been slowly upward. Although this shift in conditions is not fully documented, it is believed that only the period 1950-1955 represents use under conditions appropriate for projection into the future. Although the fit for this period is good, the base is obviously weaker than for the other series.

The reported use of "other forest areas" shows a similar pattern, but since this is largely a miscellaneous use scattered over the forests the reliability of the estimates is probably lower than for most of the other series. Whatever the reason, a heavy use of this type reported for the period 1943-1947 is shown as suddenly reduced to less than 30 percent of its previous level by 1949. From 1949 on there is a very consistent upward trend which may reflect overflow from organized facilities. Again the projection is made on a reduced base and the importance which can be attached to the projection is somewhat questionable.

Another standard Forest Service series

on recreational use of the National Forests is titled "Highways, roads, and water routes." The reported use in California shows some wide fluctuations, followed by a very rapid increase from 1951 through 1955. This series is based on estimated travel on highways and roads passing through National Forests, excluding a limited number of major routes of travel (such as U. S. Highway 40) but including other primary highways (such as U. S. Highway 50) as well as secondary highways and roads. What, if any, meaning can be attached to this form of "use" is not clear to the writers. In addition, it is probable that the series is much less reliable than most of the other recreational use series. For these reasons these data were not analyzed.

Similarly the Forest Service series on total recreational use has been dropped from the report. This series is affected by each of the reporting errors and problems which have been discussed above. In addition, it is very heavily influenced by the highway and road use estimates. In 1955, for example, use of highways and roads accounts for 45 percent of the reported total recreational use of the National Forests in California.

Projections of Future Recreational Use

It has been shown that the estimating equations developed in the preceding section meet three of the four criteria necessary for statistical projections. The relationships between recreational use and California population appear reasonable; quantitative data on the variables are available over a period of time; and the correlation between the variables has been found to be significant. There remains the question of the direct projection of the independent variable into the future.

Various demographic studies have been made which provide a basis for estimating the future population of California. In this analysis use was made of the population projections published by Stanford Research Institute (Nielson, 1955). These projections are recent, carefully prepared, and widely used within the state. They indicate that California's population, which amounted to 6.34 million in 1936, to 9.55 million in 1946, and to 13.03 million in 1955, will have risen to 15.63 million in 1960 and to 18.06 million in 1965.

By using these projected populations for 1960 and 1965 in the estimating equations (Table 1) it is possible to project the level of these particular forms of forest recreation through 1965 (Table 2).

In presenting these projections, it is necessary to stress that these are projections of what *may* occur, not predictions of what *will* occur. They are the products of the assumptions from which they were derived. Thus, each projected recreational use level indicates the amount of use to be expected in 1965 if California's population is 18.06 million and if the relationships between recreational use and population over the next 10 years are the same as they have been over the last decade.

The question of whether or not the relationships between recreational use and population which existed over the last 10 years are likely in fact to continue in the future deserves some exploration. The visitor and visitor-day figures used in this study are in reality simple physical measures of consumption. In economic terminology, consumption is the resultant of both supply and demand, and changes in consumption result from changes in the relationship between supply and demand. Since the estimating equations are derived from past consumption changes, they have a "built-in" allowance for the particular pattern of change in relationship between demand and supply which occurred in the past. Thus the projections postulate a continuation of this particular rate and direction of shift between supply and demand. If supply in the future expands more rapidly relative to demand than it has in the past, then actual use in the future should exceed the projections, while if the opposite is the case use will be held below the projections.

Thus it is desirable to consider briefly some of the indications of the supply situation over the last 10 years. Only the Forest Service data will be considered in this connection.

The best simple indicator of "supply" of recreational use opportunities in the National Forests is the inventory of recreational areas and facilities which is compiled at 5-year intervals (Table 3). The supply situation indicated is in very sharp contrast with the rising consumption trends which have been shown. In only one category has there been an increase in facilities in any way comparable to the increase in use, while in some important groups the physical quantity of facilities has actually decreased over the period. And these data do not reflect the deterioration in the condition of the remaining facilities which is also an important aspect of the supply situation.

Camping and picnicking, which in 1955 constituted 40 percent of the total use of the eight classifications analyzed, provide an important example of the relationships

TABLE 2. Recreational use, as reported and as projected, selected years, 1946-65.

Type of Use	Reported			Projected	
	1946	1950	1955	1960	1965
			Thousands of Visitors		
National Parks:					
Yosemite	640	821	984	1300	1540
Kings Canyon and Sequoia	537	717	1070	1510	1880
Lassen Volcanic	99	184	304	430	551
Total	1276	1722	2358	3220[1]	3950[1]
			Thousands of Visitor Days		
National Parks:					
Yosemite	1890	2360	2570	3130	3540
Kings Canyon and Sequoia	840	1080	1570	2170	2690
Lassen Volcanic	135	253	396	557	713
Total	2865	3693	4536	5860[1]	6940[1]
National Forests in California:					
Campgrounds	3885	4132	5959	7650	9230
Picnic areas	300	509	855	1190	1540
Winter sports areas	395	406	1302	1660	2220
Organization camps	1645	989	1399	1760	2100
Hotels and resorts	1640	480	768	1170	1500
Recreational residences	1947	1779	3056	3840	4710
Wilderness areas	160	224	413	655	850
Other forest areas	3972	1611	3463	5300	7120
Sub total	13944	10140	17215	23230	29270
Roads and water routes	6281	5065	13857	Not projected	
Total	20225	15195	31074	Not projected	

[1]Totals projected separately and do not equal sum of individual Park projections exactly due to rounding errors

TABLE 3. Recreational Areas and Facilities in National Forests in California.

Type of Area	Number of Areas			Normal Capacity at One Time, Thousands of People		
	1946	1950	1955	1946	1950	1955
Campgrounds	935	947	958	37.7	41.6	42.0
Picnic areas	59	55	74	8.1	7.7	5.3
Camp and picnic areas	119	61	92	17.2	13.5	13.7
Swimming areas	36	39	48	6.0	6.8	9.9
Winter sports areas	51	48	53	79.6	79.9	90.9
Organization camps	152	181	217	20.2	18.4	24.2
Hotels and resorts	159	137	152	11.8	7.4	8.5
Recreational residences	7529	8325	7770	40.9	49.7	51.9

involved. The normal capacity at one time of all the camping and picnicking facilities has declined from 63 thousand people in 1946 to 61 thousand people in 1955 while the use of such facilities increased by about 60 percent over the same period. The annual number of visitor-days of use per man unit of normal capacity at one time for a particular type of facility might be termed the *use factor*.[2] This use factor for camp and picnic areas rose from 66.4 in 1946 to 73.9 in 1950 and on up to 111.7 in 1956. Whatever effect this increasing intensity of use has had in checking expansion of consumption is reflected in the historical record of use which is projected into the future. Thus in effect the projected level of use in 1960 and 1965 is a level consistent with a continuance of these trends for intensified use of facilities. If facilities are expanded so that use ratios in the future are held below this rising trend, then the amount of use to be anticipated would be higher than that projected.

To appreciate the full significance of this conclusion, it is necessary to keep in mind the present condition and use of these facilities. Use is by no means equally distributed among the facilities, and the impact on certain of the better known and more accessible areas is extremely heavy. Use of some of these areas on holiday weekends has frequently run as high as 5 times the designed capacity and peak loads of 10 times capacity have been reported for a few sites.

In the case of winter sports, there was about a 14 percent increase in the normal capacity of the facilities during the period 1950-55, but use expanded considerably more rapidly than this. The use factor, which ran around 5 during the first part of the post-war period, had more than doubled by 1955. Thus the projected annual use in this case reflects use to be anticipated with some further expansion of facilities but with continued intensification of the use of facilities. Actually, increased facilities now under development apparently will raise the rate of increase above that reflected in the projection, and use higher than that projected can be expected.

In organization camps the expansion of capacity in recent years has generally par-

[2]This use factor is a measure of the intensity of annual use and does not reflect short period peak use loads which are a serious administrative problem. For example, if use were uniformly distributed for a facility available for use throughout the year, a use factor of 365 would simply indicate full use at designed capacity. Actually, use is concentrated in certain short periods and many facilities can be used only on a seasonal basis. Thus use substantially in excess of capacity may occur for short periods even though annual use rates appear low in absolute terms.

alleled the expansion in use, and the use ratio has run around 55. Thus the projection anticipates a proportionate increase in supply, and unless this occurs it is probable that the projected levels will not be realized. Hotels and resorts show a 14 percent increase in capacity from 1950 to 1955, but the increase in use was greater and the use factor rose from 65 to 90. As in the case of winter sports areas, the projection reflects increases both in capacity and in intensity of use.

In the case of recreational residences, the 25 percent increase in capacity from 1946 to 1955 apparently reflects increased capacities of the individual residences, since the total number of residences first rose but then fell back nearly to the earlier level. Again the intensity of use rose over the period, with the use factor rising from around 40 to nearly 59 by 1955. Here again the projection reflects both intensification of use and increases in capacity, whether through additional residences or further expansions of existing residences.

Implications of the Study

This study has shown that there are data available on the recreational use of public forest lands which are usable in statistical analyses and projections of the consumption of this particular type of forest service or benefit. Such data exist in greater detail than was used in this analysis. National Park data include information on certain uses within the parks. Forest Service records are for individual forests and ranger districts. Analysis of these data could add significantly to the knowledge of use patterns and the factors which control them. It is apparent, however, that any such data would need to be carefully scrutinized prior to carrying out the analysis in order to eliminate the effects of gross reporting errors and special conditions.

The bases for estimating and collecting these recreational use data have been improving over the years. However, additional precision in definitions and refinements in methods of estimation are needed.

A more important consideration is whether or not the kinds of data collected will provide the basis for the types of analytical results needed. This involves questions as to the possible usefulness and limitations of the type of analysis developed in the preceding sections.

Probably the most significant limitation on the results of such an analysis is the fact that the statistical projections are projections of consumption records, not of demand. At best, they are simply the logical extension of our past practices under anticipated population developments. As projections of consumption they are subject to modification by policy decisions or administrative actions which would change either the supply or the demand determinant of consumption. The projections show where the types of practices we have followed up to now are taking us, and thus should be useful in decisions as to whether or not changes in these practices are desirable. They do not, however, show the results to be expected under changed practices.

For example, in approaching the problem of planning future recreational facilities it would be helpful to know the intensity of use to be anticipated. For this purpose the levels of use projected for an anticipated California population of 18 million by 1965 might be reviewed. The indicated increases in use in 1965 as compared with 1955 are as follows:

National Parks	
Yosemite	38 percent
Sequoia and Kings Canyon	71 percent
Lassen Volcanic	80 percent
National Forests	
Campgrounds	55 percent
Picnic areas	80 percent
Winter sports areas	71 percent
Organization camps	50 percent
Hotels and resorts	95 percent
Recreational residences	54 percent
Wilderness areas	106 percent
Other forest areas	106 percent

Does this mean that if these various kinds of facilities are expanded by corresponding percentages the pressures of use on facilities would then be the same in 1965 as in 1955? The exact answer will vary according to use, but generally the answer would be that *such a percentage increase in facilities would be accompanied by a volume of use higher than that projected.* Campgrounds provide an important instance of this. The expanding use of Forest Service campgrounds which has been projected has actually been based on a declining resource, so a 55 percent increase in campground facilities would involve a type of alteration of supply which cannot be reflected by statistical projections of past use. Only a direct study of demand could provide the answer as to the level of use to be expected under various possible levels of facilities which might be provided in the future. The projections show only the level of use to be expected if past trends in supplying such facilities are continued in the future. However, it is believed that even such a limited answer can be useful in planning if it is properly interpreted.

The physical aspects of recreational facilities such as number of facilities and their state of repair which have been stressed in this analysis, refer mainly to the qualitative aspects of the benefit supplied. Changes in these items involve changes in the supply schedule. But shifts in supply can also be made through changes in the monetary cost of use. Currently, use of these facilities is available either free or at a service charge which commonly is low, with the major part of the costs being paid from general revenues rather than by the individual users. If in the future the policy decision were made to shift these costs to the users through sharp increases in fees, the imposition of a recreational use license, or similar devices, then the level of use would be less than it would be if the same quantity of facilities were to be provided from general revenues. Again, the type of analysis possible from the data considered here cannot give the answer as to how much decrease in use would be involved in this type of supply change.

Such possibilities of altering future use from the projected trends through changes in the quantity, quality, or costs of the supply aspects are probably fairly obvious. Possibilities of changing the demand schedule may also deserve mention. One such possibility would be to expand recreational opportunities on private forest land so that recreational demand would be shifted to some extent from public to private areas. Presumably this would require the development of an institutional environment that would enable the owner to obtain an income from the service rendered.

These and many similar issues that could be raised involve questions in public policy related to both land use and the significance of forest recreation to society. Statistical projections of past use cannot provide answers to these issues, but they can contribute to an understanding of where we are now headed.

Although there are data on recreational use of forest lands which can be used in statistical analyses, it is apparent that any comprehensive analysis would be plagued by many problems of data. Statistics on forest products are far more abundant than those on forest recreation, yet studies of future consumption of forest products such as those recently made by Stanford Research Institute (1954) and the U. S. Forest Service (1955) have shown inadequacies of data to be an abundant source of difficulties. In comparison, the difficulties in any comprehensive study of forest recreation appear to be truly formidable.

Generally the public agencies administering forest areas on which large scale recreational use is carried out have recognized the importance of data on this use. On private lands, however, there is very little information to indicate the intensity of recreational use. Unless such data are recorded and made available, there is a real danger that analysts concerned with comprehensive studies of forest recreation will necessarily concentrate on public lands with-

out being able to give equal consideration to the present and potential contributions of private forests to this type of use.

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The Structure of Wood

By. F. W. Jane. The Macmillan Co., New York. 427 pp. illus. 1956. $9.50.

Review by Everett Ellis
University of Michigan, Ann Arbor

This new book, although primarily concerned with wood structure and anatomy, also covers many other subjects of interest to the practical wood technologist. The species used to illustrate many sections will likely be unknown to the average American worker as will be many descriptive terms. The book includes 17 chapters, an appendix, a bibliography, and an index. Chapter sub-headings are rarely used, making for difficult reading. Excellent photomicrographs and line drawings, illustrate specific references to tissues or examples.

The introductory chapter lists an unusually large number of classified plant genera. Five chapters are concerned with details of anatomical wood structure, for softwoods (conifers) and hardwoods (dicots). Illustrations of cross field pitting in conifers are particularly well done, as are diagrams of heterogeneous and homogeneous hardwood rays. The terminology employed in classifying hardwood parenchyma arrangements is confusing to the reviewer.

Chapter 7 interestingly describes and illustrates atypical trees and woods. There follows a brief sound condensation of present knowledge of the "ultimate structure of wood." Consideration is next given to variability of wood, reaction wood, and diseased wood, the latter disappointingly brief. Chapter 10 admirably explains figure in wood. The following chapter discusses properties and uses of wood in relation to its structure; the difficulties inherent in predicting properties and uses based on structural considerations are detailed fully.

Identification of wood is introduced by a description of the difficulties involved and of the lack of reliable information. Attention is then directed to identification of common hardwood and softwood timbers in two well-illustrated chapters. Special consideration is given to the separation of important commercial groups appearing in the trade as teak, mahogany and walnut; oaks, ashes, and maples (and certain eucalypts) are similarly treated in the last chapter.

An Appendix gives a brief but capable account of microtechniques embracing softening, sectioning, staining and mounting. A good bibliography and a thorough index make the book much easier to use.

Structure of Wood should be of interest to the advanced student of wood anatomy or wood technology and to many practicing wood technologists; it would not be satisfactory text for the novice. The book's wide coverage and excellent illustrations will serve to expand the reader's knowledge and make it a valuable addition to reference sources for students and workers concerned with wood technology.

Effect of Continuous High Light Intensity On Photosynthesis of Forest Tree Seedlings

BY
THEODORE T. KOZLOWSKI

REGENERATION STUDIES in the Piedmont of North Carolina have revealed several basic differences in photosynthetic response of seedlings of loblolly pine (*Pinus taeda* L.) and competing hardwoods. Kramer and Decker (1944) found that photosynthesis of loblolly pine increased with increase in light intensity up to full light, whereas photosynthesis of competing hardwoods was greatest at one-third or less of full light intensity. The relatively low rates of photosynthesis of pine seedlings in the shade apparently result principally from mutual shading of the needles by one another (Kramer and Clark, 1947). It has been shown further that loblolly pine seedlings have a generally lower inherent capacity for photosynthesis and build up lower carbohydrate reserves than competing hardwood seedlings (Kozlowski, 1949). In addition, Bormann (1956) observed that very young pine seedlings with juvenile and secondary needles respond differently to varying light intensities than older pine seedlings with predominantly secondary needles. The young pine seedlings reach maximum rates of photosynthesis at relatively low light intensities and resemble hardwood seedlings in this respect. Furthermore, the juvenile leaves of young pine have a higher rate of photosynthesis than secondary needles, their rate approaching that for hardwood seedlings. These fundamental differences in response of competing tree species establish more clearly the physiological basis for the typical successional sequence from pure pine communities to climax hardwood forests in the Piedmont.

Since loblolly pine is particularly successful in a high light environment and fails to thrive in shade, the present investigation was initated to observe the photosynthetic response of loblolly pine and competing hardwood seedlings in an environment with several hours of illumination at high intensity. This study was conducted at Duke University, Durham, N. C.

Methods

Experiments were conducted on two-year-old seedlings of loblolly pine (*Pinus taeda* L.), Eastern red oak (*Quercus rubra* L.) and dogwood (*Cornus florida* L.). Photosynthesis of loblolly pine and eastern red oak was determined simultaneously because the apparatus could accommodate two seedlings. Eight seedlings of each species were tested on eight different days. Photosynthesis of dogwood was determined separately.

Apparent photosynthesis was measured by determining the difference in CO_2 content of an air stream before and after

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it was passed over the top of a seedling. The plant chambers used were those described by Decker (1944). Absorption of CO_2 was determined by a conductivity method using platinum electrodes that were replatinized in a solution of platinic chloride and charged with hydrogen according to the methods of Clark (1928). The apparatus was recalibrated as described by Kozlowski (1949). Fifty milliliters of approximately 0.002 N NaOH were used as a charge for the absorbent towers. This solution gave a change of 200-300 ohms during a 15-minute determination. Flowmeters of the type described by Gilbert and Shive (1941) were used to measure the volume of air samples analyzed. Air was drawn from the plant chambers at a constant rate of 0.42 liter per minute. Total flow was controlled by a separate air line and flowmeter. The standard procedure for determining photosynthesis with the apparatus and checks on its efficiency were reported earlier (Kozlowski, 1949).

A light intensity of 10 thousand footcandles, approximating full midday sunlight, was maintained over the seedlings with a battery of projector spot lamps. Eight 15-minute determinations of apparent photosynthesis were made at hourly intervals beginning at 9:00 a.m. and ending at 4:00 p.m. The lights were turned on, and the plants were subjected to a 30-minute stabilization period prior to the first determination each morning. The temperature in the shoot chambers was maintained at 25°C. Air flow was constant throughout the eight determinations for any one seedling.

Results and Discussions

Results are summarized in Figure 1. Apparent photosynthesis of each species is expressed as a percentage of the rate for the time of day when that species showed maximum photosynthetic activity. Light inhibition of photosynthesis occurred in oak and dogwood after 10:00 a.m. and in pine after 11:00 a.m. Photosynthesis of oak appeared to be especially sensitive and decreased rapidly when the decline once started. The slight increase at 2:00 p.m. is undoubtedly an artifact since only two oak seedlings showed increases while the other six seedlings showed decreases at this time. One of the oak seedlings had a large increase at 2:00 p.m. which was out of line with the performance of the seedling during the rest of the day. After 2:00 p.m. photosynthesis declined rapidly until by 4:00 p.m. it was reduced by 30.5 percent of the observed maximum. There was also a consistent decrease in photosynthesis of dogwood after 10:00 a.m., until by 4:00 p.m. it was reduced by 17.8 percent. Photosynthesis of pine followed a different pattern, increasing until 11:00 a.m. and then decreasing slowly and consistently to a maximum reduction of 11.4 percent by 4:00 p.m.

In both oak and dogwood the average differences in photosynthesis between 9:00 a.m. and 10:00 a.m. were not statistically significant. In dogwood, three seedlings had the highest rate at 9:00 a.m., whereas in oak five seedlings showed the highest rate at 9:00 a.m. For both species the

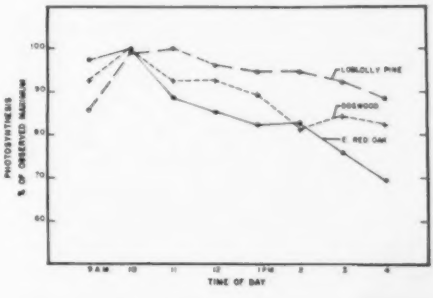

FIGURE 1. *Effect of continuous high light intensity on photosynthesis of tree seedlings. Light was maintained at 10,000 ft. candles throughout the day. A 30-minute stabilization period was used prior to the 9a.m. determination.*

higher average values at 10:00 a.m. are primarily the result of rather large increases at that time in a few seedlings only. In pine, however, the 10:00 a.m. readings were significantly higher than the 9:00 a.m. readings, but no real differences existed between the 10:00 a.m. and 11:00 a.m. values. It appears, therefore, that under the conditions of the experiment the 30-minute stabilization period was adequate for the hardwoods to achieve maximum photosynthesis but not for pine. Decker (1944) found that apparent photosynthesis of loblolly pine remained unchanged for as long as six hours when the light intensity was maintained at only 4500 foot-candles.

The results of this experiment emphasize the inhibitory effects of continuous high light intensities on photosynthesis and also stress the marked variation in response of competing pine and hardwood seedlings to such intensities. The much greater light inhibition of photosynthesis with time in the hardwood seedlings suggests that in well exposed trees inhibitory solarization may cause the outer leaves of their crowns to carry on photosynthesis less efficiently than do partially shaded leaves. Apparently Kramer and Decker (1944) observed similar light inhibition when they reported that "in preliminary experiments at 30°C the rate of photosynthesis in oaks began to decline rapidly after five or six hours at a high light intensity." They also reported an indication of decrease in photosynthesis of hardwoods as light intensity was increased from one-third of full light to full light intensity but they did not substantiate the decline statistically. Their seedlings were never exposed to any given light intensity for more than an hour and a quarter. Inhibitory effects of high light on photosynthesis were also found by Bormann (1953). He found that apparent photosynthesis of sweetgum (*Liquidambar styraciflua* L.) at 10 thousand foot-candles reached a maximum in the early morning, thereafter it declined at a fairly uniform rate. Under continuous illumination at 3200 foot-candles a maximum was reached in the midmorning and this was followed by an erratic decline.

In the present study the hardwood seedlings more typically resembled shade-adapted plants, and loblolly pine resembled light-adapted species. According to Rabinowitch (1945), light inhibition of photosynthesis can most easily be obtained in plants adapted to weak light. Photosynthesis of such individuals reaches a maximum in relatively moderate light and then declines again. Rabinowitch emphasized that in shade plants a decline in photosynthesis cannot be avoided even in short-time experiments. In sun plants, however, the photosynthesis curve flattens out beyond the saturating light intensity. But even in sun plants, prolonged and intense illumination causes inhibition in photosynthesis with time. Böhning (1949) found no falling off in rate of photosynthesis with time of continuously illuminated, light-adapted apple leaves but photosynthesis of shade-adapted apple leaves decreased with time. Böhning used a light intensity of only 3800 foot-candles over his shade-adapted plants and illuminated them both day and night for several days. But even at this relatively low light intensity, photosynthesis of shade-adapted apple leaves decreased within a day. Lundegardh (1931) also reported marked decreases in photosynthesis at high light intensities for the shade fern *Dryopteris austriaca*.

The specific causes of the inhibition and species differences in rate of decline of photosynthesis with time are not clearly identified but several possibilities exist. Rabinowitch (1945) pointed out that in shade plants complete inhibition of photosynthesis may result under intense illumination and plants may suffer irreversible injury or death by "sunstroke." Under such conditions photosynthesis may be inhibited by photo-oxidative deactivation of some of its enzymes. The rather rapid decline of photosynthesis in the present study suggests that a similar deactivation occurred

with some enzymatic destruction. Böhning (1949) concluded that such destruction of enzymes resulted in the initial decrease in photosynthesis of shade-adapted apple leaves, whereas a later decline in the same leaves and a decline in photosynthesis of light-adapted leaves were caused by reduced chlorophyll content resulting from bleaching of the leaves. Although normal fluctuations in CO_2 concentrations of the air often cause changes in photosynthesis (Böhning, 1949), it seems unlikely that the observed decreases in photosynthesis shown in Figure 1 could be mainly accounted for by decreasing CO_2 content of the air. There was a small and consistent decrease in the average CO_2 concentration in each plant chamber throughout the day. CO_2 concentration of the air was greatest at 9:00 a.m. and least at 4:00 p.m., but the greatest reduction was only 4.2 percent of the observed maximum. Outdoor air was drawn into the plant chambers from the top of the biology building because it was found in previous experiments that the CO_2 concentration of the air at that height was much more constant than at lower levels. Possibly some of the photosynthetic decrease toward the end of the day is linked to the slowly decreasing CO_2 concentration but the large differences in species response suggest that other factors are mainly involved. Furthermore, between 10:00 and 11:00 a.m., when large decreases in photosynthesis were observed, the CO_2 concentration was close to the daily maximum. Although the air temperature in the plant chambers was maintained at 25°C., there exists the possibility of an increasing chloroplast temperature throughout the day. Since thermocouples were not inserted into the leaves, this possibility cannot be eliminated as contributing through increased leaf respiration. Other possible factors involved in the observed decline in photosynthesis with time include differences in accumulation of photosynthetic products, increased respiration due to increased amounts of photosynthetic products thus causing apparent photosynthesis to be lower, bleaching of chlorophyll, stomatal closure as reported for *Coffea arabica* at high light intensities (Nutman, 1937), and decreased availability of water.

Summary

1. Apparent photosynthesis of two-year-old seedlings of loblolly pine, eastern red oak and flowering dogwood was measured hourly from 9:00 a.m. to 4:00 p.m. under a continuous light intensity of 10 thousand foot-candles.

2. Light inhibition of photosynthesis occurred in oak and dogwood after 10:00 a.m. and in pine after 11:00 a.m. The decrease in photosynthesis with time was greater in oak and dogwood than in pine. Maximum reduction of photosynthesis was observed in all species at 4:00 p.m. when the final observations were made. Maximum amounts of reduction in photosynthesis were: for oak 30.5 percent, for dogwood 17.8 percent and for loblolly pine 11.4 percent.

3. The photosynthetic reaction of oak and dogwood seedlings resembled that of shade-adapted plants while the reaction of loblolly pine more nearly resembled light-adapted species.

4. Several possible causes for light inhibition of photosynthesis and for observed species differences in photosynthetic response are considered.

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The Fungus Causing Western Gall Rust And Woodgate Rust of Pines

BY
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WESTERN GALL RUST, characterized by the development of pear-shaped to globose galls on the stems of two- and three-needle pines in the western United States and Canada, is caused by *Peridermium harknessii* Moore ex Hark. The rust also occurs in the East on jack pine, (*Pinus banksiana* Lamb.), having been found at several places in Quebec (Pomerleau 1942). Pycnia are rare but aecia are abundant on pines. Uredia and telia have been thought to occur on several genera of *Scrophulariaceae*, most commonly on paintbrush (*Castilleja* spp.) On these hosts the fungus has been called *Cronartium harknessii* (Meinecke 1920:282, 290), but it has not been validly described. It has also been called *C. coleosporioides* Arth. (Blasdale 1919: 108).

In June 1925 a gall-forming *Peridermium* on Scotch pine (*P. sylvestris* L.) was discovered near Woodgate, New York, where it had been present for at least 30 years (York 1926). Further investigations have shown the presence of this gall rust at other places in the Northeastern States and eastern Canada, and to be of long standing; at Ottawa, Ontario, it dates back to 1888 or earlier (McCallum 1929). Since the affinities of the *Peridermium* were not apparent, it was called Woodgate *Peridermium* or Woodgate rust after the place where it was first recognized. For a few years after this *Peridermium* was found it was feared that it might have been introduced from another continent and that it might become destructive to native pines. With time, as no outbreaks were found except on Scotch pine, this uneasiness largely subsided.

The fungus on Scotch pine was tentatively assigned to *Cronartium quercuum* (Berk.) Miyabe (C. *cerebrum* Hedge. & Long) by Arthur (1934:26), but there is no relation between the distribution of the *Peridermium* on Scotch pine and uredia and telia on oaks (*Quercus* spp.). The galls are frequently found on pines many miles from the nearest oaks. To one familiar with western gall rust, it seemed more probable that the gall rust on Scotch pine was the same (Boyce 1929). Both *Peridermium harknessii* and Woodgate *Peridermium* infect directly from pine to pine. Both can attack ponderosa pine and the galls resulting are identical.

Because of the economic importance of pines and because of the severe damage to them by caulicolous *Peridermiums*, an investigation was begun to determine (1)

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the possibility of western gall rust caused by *Peridermium harknessii* spreading naturally from the West to pines of the East and South, and (2) the identity of the fungus causing Woodgate rust of Scotch pine.

In the spring of 1944, species of pines with overlapping ranges from the Pacific Coast across Canada to the Atlantic Coast and thence south to the Gulf of Mexico were grown from seed in the Marsh Botanical Garden of Yale University, New Haven, Connecticut. The following species listed in the order of their natural distribution from west to east to south were established, the name of the state being the only information on seed provenance obtainable from the dealer: ponderosa pine, *Pinus ponderosa* Laws. (California); ponderosa pine (British Columbia); lodgepole pine, *P. contorta* Dougl. (Washington); lodgepole pine, *P. contorta* var. *latifolia* (British Columbia); jack pine, *P. banksiana* Lamb. (Wisconsin); pitch pine, *P. rigida* Mill. (Cape Cod, Massachusetts); Virginia pine, *P. virginiana* Mill. (Georgia); shortleaf pine, *P. echinata* Mill. (Arkansas); and slash pine *P. elliotti* Engelm. (Georgia). Scotch pine, *P. sylvestris* L. (New York) was also included. The seedlings were kept outdoors in the nursery bed except that Virginia, shortleaf, and slash pines, not being sufficiently cold resistant for the New Haven climate, were potted in the autumn of 1944, kept in the greenhouse during the winter and moved outdoors again for the growing season. This procedure was followed annually until the spring of 1948 when these three pines were set into the ground permanently in the greenhouse. Meanwhile, in the spring of 1946 the other pines were transplanted to their permanent position outdoors.

By the spring of 1948 many of the pines were large enough so that the first of three series of inoculations could begin. The inoculations in the springs of 1948 and 1951 were made with aeciospores from California, and those in the spring of 1953 with aeciospores from New Haven that developed on galls resulting from the 1948 inoculations.[1] The 1948 and 1951 inoculations were made in wounds on the stem. With a scalpel a slit about 0.5 cm. long, oriented more tangentially than radially, was made in the stem so that the cut passed through a broad area of living bark to the wood. Aeciospores were put into the slit with the same scalpel and, then the stem at the place of inoculation was

[1]The inoculum from California was supplied by W. W. Wagener, J. W. Kimmey and P. C. Lightle, necessitating special collecting trips by them. The writer gratefully acknowledges this help, without which the work could not have been done. Immediately after collection the inoculum was sent to New Haven by air mail where it was used at once or stored in an electric refrigerator until the new shoots on the pines had developed sufficiently. In some instances the inoculum was used in New Haven within four days after collection in California, in others it had to be kept for several weeks. In all cases, however, the aeciospores germinated freely in tap water just before use.

1948 inoculum: Aeciospores from *Pinus radiata* near San Mateo, California; elevation 100 feet; March 29, 1948. Aeciospores from *P. sabiniana* in Sunset Valley, Los Padres National Forest, elevation 3000 feet; May 22, 1948. Aeciospores, from *P. ponderosa* (tree No. 4A6) in grounds of Institute of Forest Genetics, Placerville, California; elevation 1750 feet; June 8, 1948.

1951 inoculum: Aeciospores from *Pinus radiata* near Burlingame, California; elevation 800 feet; March 26, 1951. Aeciospores from *P. sabiniana* in the lower Feather River Canyon, near Oroville, California; elevation 800 feet; March 24, 1951. Aeciospores from *P. ponderosa* (tree No. 4A6) in grounds of Institute of Forest Genetics, Placerville, California; elevation 1750 feet; May 18, 1951.

1953 inoculum: Aeciospores from *Pinus sylvestris*, *P. ponderosa* (British Columbia provenance), and *P. ponderosa* (California provenance); trees grown from seed in New Haven.

wrapped in moist cotton covered with waxed paper in the first inoculations and with "Parafilm" in the later ones. The wrappings were removed in about 10 days. Checks were made in the same way but no inoculum was placed in the wounds. The inoculations were made on the stem tissue of the current season, on one- two- and three-year-old stem tissue, as were the checks. The 1953 inoculations were performed without wounding on stem tissue of the current season only. The shoot and young needles were moistened, aeciospores were smeared on a portion of the shoot about one inch long and the area then wrapped in most cotton and covered with "Parafilm." The wrapping was removed in about 10 days. Checks were made the same way, but without inoculum. For the three series of inoculations, i. e., 1948, 1951 and 1953, the checks were always on inoculated trees but not on all of them. A total of 693 inoculations and 248 checks were made.

1948 and 1951 Inoculations

Results of the wound inoculations made in 1948 and 1951 are shown in Table 1. From the 665 inoculations, 41 or 6.2 percent characteristic galls developed, the criterion used for judging successful inoculations. Infections resulted in ponderosa pine (B. C.), ponderosa pine (Calif.) and Scotch pine (N. Y.) only. The other species, even including jack pine and lodgepole pine that are known to be hosts for western gall rust, were not infected. Of the 665 inoculations, 409 or 61.5 percent were made on shoots of the current season, 208 or 31.3 percent on one-year-old interwhorls, 36 or 5.4 percent on two-year-old interwhorls, and 12 or 1.8 percent on three-year-old interwhorls. The term interwhorl designates the lengths of stem between branch whorls in conifers (Kimmey 1954). Of the 41 galls resulting, 23 or 56.1 percent were from inoculations on shoots of the current season, 16 or 39 percent from inoculations on one-year-old interwhorls, 2 or 4.9 percent on two-year-old interwhorls, and none on three-year-old interwhorls; but only a few inoculations were made on the oldest interwhorls. Scanty pycnia developed on four galls and aecia on 28.

1953 Inoculations

The inoculations in 1953, made without wounding, were limited in number and hosts. They were confined to shoots of the season on 4 trees of ponderosa pine (Calif.) with 9 inoculations and 3 checks, 6 trees of ponderosa pine (B. C.) with 11 inoculations and 4 checks, and 1 tree of Scotch pine (N. Y.) with 8 inoculations and 2 checks; a total of 11 trees, 28 inoculations, and 9 checks. The inoculum was aeciospores from galls on the same host species that had developed from earlier inoculations with aeciospores from California. Inoculations on ponderosa pine (Calif.) and Scotch pine (N. Y.) were negative, as were all the checks.

Three galls developed on two trees of ponderosa pine (B. C.). The tree bearing one gall was inoculated with aeciospores from a gall on ponderosa pine that had developed after inoculation with aeciospores from a gall on ponderosa pine in California, while the tree bearing two galls was inoculated with aeciospores from a gall on ponderosa pine that had developed after inoculation with aeciospores from a gall on digger pine (*P. sabiniana* Dougl.) in California. No pycnia or aecia had appeared by the end of the 1955 growing season when these lines were written.

Galls

These experiments gave no exact information on the method of infection, except that infection developed from wound inoculations on shoots of the current season, and on one-year-old and two-year-old interwhorls, the two latter with well developed bark. Also inoculations of the shoot of the current season were successful

TABLE 1. Results of inoculating pines with aeciospores in 1948 and 1951.

Species of *Pinus*	Trees inoculated	Data an inoculations				Data on checks	
		Inoculations	Trees infected	Galls	Galls producing aecia	Checks	Galls
		Inoculum from *Pinus sabiniana*					
banksiana	3	31	0	0	0	10	0
contorta	3	22	0	0	0	11	0
echinata	4	21	0	0	0	11	0
elliottii	5	50	0	0	0	18	0
ponderosa (B. C.)	6	32	5	21	9	9	0
rigida	4	21	0	0	0	7	0
sylvestris	5	40	1	11	10	16	0
virginiana	3	16	0	0	0	13	0
Total	33	233	6	32	19	95	0
		Inoculum from *Pinus ponderosa*					
banksiana	4	37	0	0	0	10	0
contorta	4	30	0	0	0	8	0
echinata	2	23	0	0	0	7	0
elliottii	3	28	0	0	0	8	0
ponderosa (B. C.)	1	8	1	3	3	3	0
ponderosa (Cal.)	4	30	2	5	5	8	0
rigida	3	16	0	0	0	4	0
sylvestris	4	48	0	0	0	10	0
virginiana	1	15	0	0	0	7	0
Total	26	235	3	8	8	65	0
		Inoculum from *Pinus radiata*					
banksiana	3	25	0	0	0	9	0
contorta	4	26	0	0	0	12	0
echinata	4	23	0	0	0	6	0
elliottii	3	38	0	0	0	15	0
ponderosa (B. C.)	5	25	0	0	0	13	0
rigida	2	9	0	0	0	4	0
sylvestris	4	35	1	1	1	11	0
virginiana	3	16	0	0	0	9	0
Total	28	197	1	1	1	79	0
Grand Total	87	665	10	41	28	239	0

without wounding. It seems probable that most natural infections occur through unwounded tissue, either through needles or through the epidermis of the young shoot before bark forms. It seems unlikely that the germ tubes of aeciospores can penetrate dead bark. Earlier investigators concluded that inoculation occurred through the tender tissue of young shoots before bark formation.

Development of the galls was the same on ponderosa pine of British Columbia and California provenances as well as on Scotch pine, and was characteristic in every way both of western gall rust caused by *Peridermium harknessii* and of Woodgate rust.

The first evidence of infection was a slight swelling of the stem, not sufficiently characteristic to be definitely diagnostic without a microscopical examination of the bark for typical hyphae. No discolored spots appeared on the stems following inoculation by wounding. Since there was no opportunity during the remainder of the growing season to observe the stems inoculated in May and June without wounding, it is not known whether or not any discolorations of the shoot of the current season developed like those described on Scotch pine by other investigators (Hutchinson 1935: 824, True 1938:26).

The incubation period (i. e., the elapsed time between inoculation and the first appearance of a swelling) was variable. For wound inoculations the period was commonly about 12 months. From a successful inoculation made in the spring, a slight swelling usually appeared the next spring. However, from an inoculation on ponderosa pine made April 6 there was a marked swelling by August 25 of the same year, and from two wound inoculations on Scotch pine made April 6 there were slight swellings by August 25; a period of about four and one-half months. All three swellings later developed into typical galls. At the other extreme, an inoculation made on Scotch pine June 9, 1948 was not recognized as successful until May 7, 1952, when a single aecium appeared on a tiny gall which until then had been considered to be a callus. The elapsed time was almost four years. Two successful inoculations on a ponderosa pine were not recognized as such until aecia appeared almost three years later, because the swellings were so insignificant. Following several other inoculations the first swelling did not appear for two years. Furthermore, the appearance of a slight swelling did not always indicate a successful inoculation. For example, a slight swelling appeared a year after an inoculation on a ponderosa pine, but a year later the swelling was no longer apparent because of the increased thickness of the stem, and no gall ever developed. Actually, it was usually 12 months after a swelling first appeared before a characteristic gall had formed, or in other words, two years after inoculation. Consequently, it was generally about two years before a reliable macroscopic diagnosis could be made of the result of an inoculation. The successful inoculations without wounding produced the first swelling in one or two years.

The mature galls were globose or semiglobose in shape, depending on whether they completely or partially encircled the stem. After aecial production, the bark broke away from the galls in large scales leaving a collar of dead bark standing out around the upper and lower end of the gall. Witches-brooms formed just above several of the galls.

Pycnia

Pycnia developed sparsely. Four galls produced pycnia once. The pycnia appeared in the spring prior to the general production of aecia. Pycnia were not repeated on the same gall for two or more seasons as were aecia. Two galls on two ponderosa pines of British Columbia provenance each had a single drop of pale amber-colored, sticky pycnial exudate about the consistency of thin syrup three years after the inoculations were made. Aecia never developed on these two galls. Another ponderosa pine, California provenance, had a gall with a single drop of pycnial exudate two years after inoculation which was followed by aecia one year later. A Scotch pine had a gall with two well separated pycnial drops that appeared on April 30, three years after inoculation, and these drops were followed by aecia on the opposite side of the gall on May 3 of the same season. From these scanty data no conclusions can be drawn except that pycnia develop occasionally and precede aecia when they do appear.

Aecia

Aecia developed on 28 galls. It was only two or three days from the time immature aecia were first visible until they were mature and ruptured, usually during the first few days of May. Aeciospore discharge generally continued until the first days of June, or for about one month. First discharge was heaviest, then it gradually declined until it stopped entirely and the aecia disintegrated. The period from the date of inoculation until the first aecia appeared varied from about 2 to 6 years, 3 years being the usual time. No aecia developed in one year following inoculation. The first aecia appeared in 2 years on 6 galls, in 3 years on 14 galls, in 4 years on 3 galls, in 5 years on 3 galls, and in 6 years on 1 gall, a total of 27 galls. No galls bore first aecia after 6 years. The one example omitted from this computation was of a different rust fungus as explained in the succeeding paragraph. On the other 27 galls, aecia appeared once only on 10 galls, for 2 successive years on 5 galls, for 3 years on 10 galls, and for 4 years on 2 galls. No gall had aecia for more than four successive years.

The aecia were large and became confluent over considerable areas, causing the bark to slough off in large scales. These were the types of aecia resulting from the successful inoculations of ponderosa and Scotch pine with aeciospores from galls on ponderosa and digger pines. However, on one gall on Scotch pine resulting from inoculation with aeciospores from Monterey pine (*Pinus radiata* D. Don), the only successful inoculation on any host with inoculum from Monterey pine, the aecia which first appeared three years after inoculation and then reappeared twice more at intervals of one year were smaller and irregularly scattered, somewhat suggesting those of the eastern *Cronartium quercuum* (*C. cerebrum*). There were no bark collars formed on this gall. This strongly supports, or even proves, Meinecke's (1929) idea that the gall-forming *Peridermium* on Monterey and other lowland pines in California is a distinct species for which he used the name *Peridermium cerebroides* (?), *P. harknessii* being confined to ponderosa and other pines of the higher elevations. Since Meinecke did not give a valid description, *P. cerebroides* (?) is a nomen nudum. A slight doubt has existed that the apparent differences between the two *Peridermiums* might be caused by differences in hosts, but in this instance the differences were still expressed on the same host. Furthermore, both forms have been found on digger pine, a tree that in California ranges from the shore of the Pacific Ocean to elevations of over 5000 feet in the Sierra Nevada (Mienecke 1920:285).

Discussion

The objectives of this investigation, i.e., to determine the identity of the fungus causing Woodgate rust and to explore the possibility that western gall rust caused by *Peridermium harknessii* had spread naturally from the West to hard pines of the East and could spread to those of the South, were only partially attained. The results of the inoculations, though somewhat meagre, are valuable.

Peridermium harknessii causing western gall rust on ponderosa and digger pines also causes the Woodgate rust on Scotch pine. The gall rust on Monterey pine is caused by *Peridermium cerebroides* (?), a gall rust that can also infect Scotch pine, although to my knowledge it has never been found occurring naturally on this host. The variation in susceptibility between individuals within a species, that is so apparent under natural conditions, particularly with Scotch pine, was fully borne out by these inoculations. Of the 13 ponderosa pines inoculated with aeciospores from digger and ponderosa pine, 8 became infected. Some of the uninfected individuals as well as the infected were inoculated both in 1948 and 1951. Of the 8 Scotch pines on which the same inoculum was used, only

1 tree was infected, but 8 of the 9 inoculations made on that tree in 1948 were successful, and in 1951 3 galls developed from 5 inoculations. This tree was susceptible whereas the other Scotch pines, some of them also inoculated in both 1948 and 1951, were resistant. The differences shown in these experiments must be inherent in the individual trees, because the inoculum was the same for different trees and the inoculations were made within a few days of one another. Actually, in some instances the same inoculum was applied successfully to one tree and unsuccessfully to another only three feet away within the same half hour.

The failure of inoculations on lodgepole and jack pines was disappointing, for if the inoculations had succeeded, it would have been a strong indication that *Peridermium harknessii* had spread naturally from West to East since the ranges of these two trees overlap, and combined they extend from the Pacific to the Atlantic Coast. Lodgepole pine is a common natural host for *P. harknessii* in the West and what appears to be this fungus has been found on jack pine in Quebec, a fact which still points to the possibility of natural spread. Inoculations on pitch pine were unsuccessful. The range of this pine overlaps that of Virginia pine which in turn connects with the other hard pines of the south. Since *P. harknessii* has been in New England for at least 80 years and has never been found on any of the southern pines within their range, it seems unlikely that it will spread to them naturally. Loblolly (*P. taeda* L.), slash, and Virginia pines have been successfully inoculated (York, 1928) so that the fungus still must be considered potentially dangerous to the South, if it should be introduced there.

Peridermium harknessi has been in the northeastern United States for a long time. It was first found by Harkness and Moore on ponderosa pine in the vicinity of Colfax, California, May 26, 1876. Harkness, through J. P. Moore, transmitted a letter discussing the fungus together with a specimen to the San Francisco Microscopical Society before which the letter was read and the specimen displayed (Harkness 1876). On June 28, 1876, Harkness received a *Peridermium* from Prof. W. G. Farlow of Harvard University accompanied by the following enquiry, "I send you a specimen of *Peridermium*, which is attacking the *Pinus ponderosa* of this vicinity. Do you find it in California?" Harkness goes on to state that, "as the specimen sent by the Professor agrees in every essential particular with the one sent to the Society, it would appear that the fungus is attacking the forests in the eastern as well as the western portion of the United States." This indicates that ponderosa pine was somewhat common at that time around Cambridge, Massachusetts. This idea is substantiated by the fact that Gray included ponderosa pine in his, "Field, Forest and Garden Botany, published in 1868 (Gray 1868). On page 311 there is a brief description of ponderosa pine with the statement, "Planted from California." On the same page there is a brief description of Scotch pine. This volume comprised common plants east of the Mississippi River, and since in the preface Gray stressed the fact that the only exotics included were "commonly cultivated or planted for ornament or use," this shows that ponderosa and Scotch pines were relatively common, at least in some parts of the East, one hundred years or more ago, so that with *P. harknessii* on ponderosa pine, Scotch pine would soon have been exposed to it. Today, ponderosa pine is a rarity anywhere in the East.

Peridermium harknessii was not actually described until 1884 (Harkness 1884) and by that time Monterey pine (*P. insignis* = *P. radiata*) and digger pine, in addition to ponderosa pine, were listed as hosts. The fungus was said to be particularly abundant at Monterey, California, which is the native habitat of Monterey pine. Neither

ponderosa nor digger pines occur there. No distinction was made between the *Peridermium* on Monterey pine and on digger and ponderosa pines, although the last sentence by Harkness in this brief account of *P. harknessii* may be significant: "The different species of Peridermium of the pine seem to be doubtfully distinct." This may imply a lack of certainty in the mind of Harkness that *P. harknessii* as described was a single species.

The host relationships of *Peridermium harknessii* have long been obscure. On pines it appears that two species of *Peridermium* were unwittingly combined under this name. The situation was further complicated by the fact that at least two species of *Cronartium* occurred within the range of *P. harknessii*, both of which have been suspected of being its perfect stage. Unless there is a definite correlation between the abundance of uredia and telia on a host for a *Cronartium* and the abundance of aecia on nearby pines, too much significance must not be attributed to the presence of some uredia and telia on any host for a *Cronartium* in the identification of a caulicolous aecial stage on an associated pine. It is known that aeciospores of *C. ribicola* Fisch. can be wind borne 300 miles or more to infect the leaves of susceptible currants and gooseberries. Consequently it is reasonable to suppose that aeciospores of some other *Cronartiums* can also be carried great distances by wind.

For example, the leaves of various oaks in California are hosts for a *Cronartium* that is widespread there. Never developing abundantly in a locality, it may or may not be associated with a *Peridermium* causing gall formation on a pine. When *Peridermium harknessii* on ponderosa pine was found at times associated with this *Cronartium* on oaks, it was thought that the oak *Cronartium* might be the perfect stage of *P. harknessii*. Actually the perfect stage of *P. harknessii* is now thought to occur on *Castilleja* and other members of the Family Scrophulariceae, and it has been called *Cronartium harknessii* and *C. coleosporioides*. Again, *Peridermium cerebroides* (?) on *Pinus radiata* is often associated with the same *Cronartium* on oaks, but inoculations from pine to oak have not succeeded (Meinecke 1920:280; 1929:328). This *Cronartium* on oak still remains unconnected. On the evergreen oaks it can overwinter in the uredial stage, thereby living without an alternate host, but it has also been found to a limited extent on deciduous oaks where this means of overwintering would not be possible unless it vegetated in the buds. It could also spread by urediospores from evergreen oaks to nearby deciduous species. However, to one familiar with western *Cronartiums*, long distance spread of aeciospores from some *Peridermium* to oak seems a likely explanation, although no particular *Peridermium* suggests itself.

Peridermium harknessii is locally quite destructive in the West to seedlings and saplings of lodgepole and ponderosa pines. Some trees are killed but far more are stunted and malformed. *Peridermium cerebroides* (?) behaves the same way on Monterey pine. However, these species of trees in their native habitats have lived with these rust fungi for a long time, so that a balance has been established that does not result in the complete destruction of a stand of forest trees but merely a greater or lesser reduction in the amount of usable timber produced. The most serious menace of *P. harknessii* is its potential danger to pines elsewhere in the world. Scotch pine in the East has been considerably damaged, but this species will never be of more than minor value in North America. However, in Europe where it is native, it is one of the two most valuable conifers economically. The tree has a wide distribution throughout Europe, and into western and northern Asia. An attack by *P. harknessii* in these two areas would be extremely serious, because even though the rust could finally be controlled since some

trees are highly resistant or immune, management plans would be completely disrupted and yields would be reduced for decades. Chir pine, or long-leaved Indian pine, (*P. roxburghii* Sarg.), of the Himalayas, because of its resemblance to ponderosa pine in habitat and gross appearance, suggests a likely host for *Peridermium harknessii* or for *P. cerebroides* (?) since the latter has been found on Canary Island pine (*P. canariensis* C. Smith) growing in California (Boyce 1943:356). Chir pine and Canary Island pine are closely allied. Aleppo pine (*P. halepensis* Mill.) is extremely susceptible to *P. cerebroides* (?) as shown by heavy natural infection of this tree at several places in California.[2]

Peridermium harknessii is particularly dangerous to pines elsewhere in the world, because new galls cannot usually be recognized with certainty until a year after infection, and in some instances until two, three, or even four years after infection. Consequently, inspection could not prevent the fungus from being introduced into new localities on living trees, so that the only sensible protection is to prohibit the importation of hosts of the fungus from regions where *P. harknessii* occurs.

Summary

Inoculations show that Woodgate rust of Scotch pine, frequent in the northeastern United States and in eastern Canada, is caused by *Peridermium harknessii*, a species common on two- and three-needle pines in western North America, where it causes western gall rust. In addition, further proof is given that *P. harknessii* occurs on ponderosa, lodgepole, digger, and other pines of higher elevations in the mountains whereas Monterey and other pines at lower elevations along the California coast are attacked by *Peridermium cerebroides* (?) that causes similar galls.

[2]Communicated by W. W. Wagener.

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Construction of Forest Roads

Forstlicher Strassen- und Wegebau. By *Franz Hafner. George Fromme & Co., Vienna and Munich. 379 pp., 316 figures, 90 tables. 1956. $6.40 (paper cover), $7.15 (cloth).*

Grading-equipment in the Construction of Forest Roads

Planiergeräte im forstlichen Strassen- und Wegebau. By Franz Hafner and Walter Hedenigg. (Schriftenreihe der forstlichen Bundesversuchsanstalt Mariabrunn, Vienna, vol. 5) George Fromme & Co., Vienna and Munich. 76 pp., 33 figures, 34 tables. 1956. $1.90.

Review by Herbert I. Winer
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The years since World War II have seen great changes in the practice of road-building in European forests. Just as on this continent, increasingly intensive forest management requires a road net of increasing density and quality, to be built in the face of constantly rising costs.

These two new volumes deal mainly with Austrian conditions and experience, with special emphasis on the problems of road construction in mountainous regions. The reader is impressed by the increased activity that has occurred in Austrian forests and by the even greater increase in the use of heavy equipment in road-building. Improved cable systems for minor transportation have stimulated the construction of main-haul roads in many hitherto inaccessible areas. All this reflects a growing pressure on that Austrian forest resource, together with an increase in real wages that now justifies the use of expensive machinery, often

imported from the United States. Thus, the gap between road-building practices in Austria and North America is rapidly narrowing.

Forstlicher Strassen- und Wegebau complements Professor Hafner's *Die Praxis des neuzeitlichen Holztransportes*, published in 1952, which dealt with log transportation as a whole. The present volume is also a textbook and reference manual, intended for the use of students, foresters, and forest engineers.

The first section of the book is an excellent account of the principles and techniques involved in planning, surveying, and costing forest roads. This theoretical foundation is firmly grounded in both European and American literature. In view of his primary concern with mountainous regions, the author wisely stops short of including elaborate formulas for road-spacing, which occasionally seem to promise more than they can fulfill.

The second section, occupying more than half the book, deals with the details of road design and construction, including drainage works and other protective structures, and the construction and maintenance of various improved road surfaces. Again, Professor Hafner has drawn widely from the literature, but he has supplemented and modified published data in order to develop many standard tables, applicable to specific Austrian conditions. These standard tables furnish valuable information on the effects of slope, soil conditions, and other factors on the performance of road-building equipment. The treatment in this section is generally fuller than in Silversides' *Construction and Maintenance of Forest Truck Roads*. In some places the author approaches the level of detail found in the *Truck Trail Handbook* of the U. S. Forest Service.

A well-selected bibliography of 290 items completes the volume.

The second volume is devoted almost entirely to the characteristics and performance of bulldozers, angledozers, and motor graders. Most of the data apply to Caterpillar tractors ranging in size from the D-2 to the D-7 (32 to 81 drawbar hp.).

In addition to standard tables on performance and costs derived from the literature, the authors include data from their recent well defined variations in equipment and series of 37 short studies conducted in Austria. These studies involved a wide range of working conditions. The reader is thus better able to predict productivity and costs in specific situations. He should also gain a deeper appreciation of the residual errors still inherent in such predictions.

Because the authors' studies seldom covered a period of more than 3 hours, their conclusions admittedly underestimate the importance of various elements of non-productive time, which may require that productivity values be reduced by as much as 50 percent in order to make them applicable to typical long-run operations. The authors conclude that further study and analysis are essential to correcting the physiological, mechanical, and organizational factors that hold actual productivity far below its theoretical level.

Unexplained Brooming of Douglas-Fir and Other Conifers in British Columbia and Alberta

BY
D. C. BUCKLAND
JOB KUIJT

IN MANY PARTS OF ITS RANGE, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) exhibits a type of brooming the cause of which is as yet unknown. This brooming was first reported from the western United States (Coheen, *et al.*, 1951). No large area of the Canadian geographic range seems to be without this phenomenon, for the brooms have been found sporadically from the Pacific coast to the Alberta foothills (see Fig. 8). They are nowhere common, however, although two or three may sometimes be found relatively close together.

Appearance of the Broom on Douglas-fir

The location of a broom on the tree varies considerably. It may occur as a small sphere of 2-3 ft. in diameter at the tip of some large, otherwise normal branch, sometimes seemingly suspended from it. It may make up the middle section of a tree's crown, the branches above and below being quite normal, though often with sparse foliage (Fig. 1). The most striking of all positions is the terminal one, where the entire upper crown is broomed (Figs. 2 and 3) and normal growth does not occur above this crown. The broom is commonly of a much darker green than the rest of the tree.

The density of the brooms also varies to some extent. A small, 1-ft. broom collected at Lasqueti Island, B. C., and deposited in the Forest Pathology Herbarium of the University of British Columbia, was completely solid because of accumulated branchlets and leaves. Terminal brooms are often so dense that very little light can be seen through them, and they may have a peculiar rounded appearance (Fig. 2). More diffuse types, however, do exist (Fig. 3). Whether this degree of compactness is related to the age of the broom is not known.

A consistent feature is the lack of gradation from normal branches to broomed ones. The broom invariably shows itself as a distinct unit, sharply delimited from the unaffected part of the tree. This appears to disqualify the idea that the brooming is nothing more than a stunting caused by locally severe climatic conditions. Also, any dominance of leaders over lateral branches seems lost, and

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Based upon work initiated by the senior author, Associate Professor of Forest Pathology at the University of British Columbia, who died February 15, 1956. The junior author, now the Department of Botany, University of California, Berkeley, accepts all responsibility for this report. Thanks are due to E. C. Darwin of Lasqueti Island for the collection of material, to Dr. Vidar J. Nordin and staff, Laboratory of Forest Pathology, Calgary, Alberta, and Mr. H. Sweet of Vancouver for various technical assistance.

FIGURE 1. Pseudotsuga menziesii *with sub-terminal broom. Seebe, Alberta.* FIGURE 2. Pseudotsuga menziesii *with terminal, compact broom. Between Golden and Radium, B. C.* FIGURE 3. Pseudotsuga menziesii *with terminal broom of the more diffuse type. Slocan Lake,* B. C. FIGURE 4. Pseudotsuga menziesii. *Branches of a broom collected at Lasqueti Island, B. C.* FIGURE 5. Picea glauca *with terminal, compact broom on a tree ca. 20 ft. high. Seebe, Alberta.*

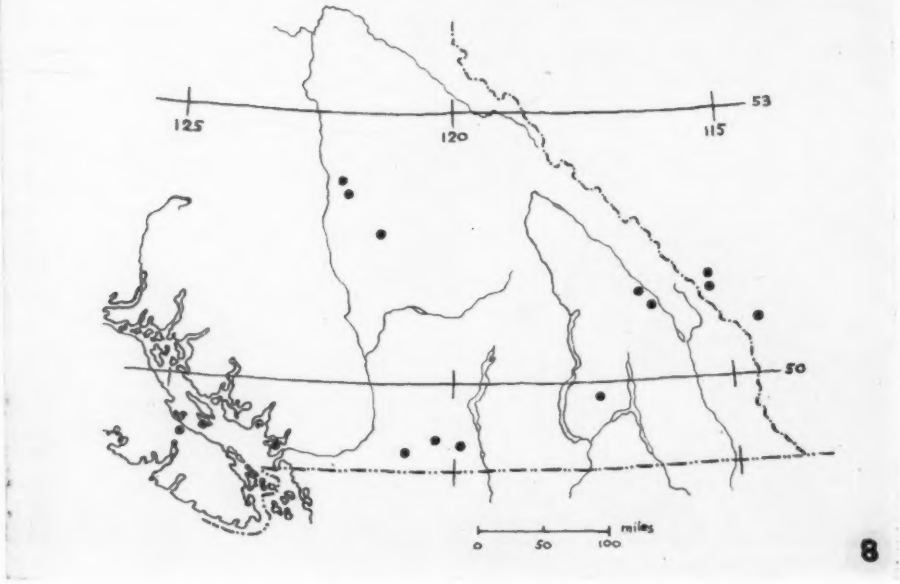

FIGURE 6. Larix occidentalis *with a large broom in the lower half of the crown. Kimberley, B. C.* FIGURE 7. Larix occidentalis. *Completely broomed tree among normal individuals. Kimberley, B. C.* FIGURE 8. *Map of southern British Columbia and adjacent Alberta showing the localities where Douglas-fir brooms as described in the text have been found.*

all branches of the broom become equivalent in this respect. This is in contrast, perhaps, to Hintikka's observations (1933) on the progeny of a broom on *Pinus sylvestris*, where he found the leaders of the broomed seedlings still distinguishable.

Close inspection reveals that shortening of internodes and leaves rather than excessive branching supplies the characters of the broom. In fact there seems to be a reduction of lateral-bud development in at least some cases (Fig. 4). Where this is true we can not speak of proliferation of branches as previously reported (Coheen, *et al.*, 1951). The above mentioned photograph shows a branch of a broom collected at Lasqueti Island. It is typical of the material inspected in that its internodes are shortened, leaves are spaced more closely, the whole presenting a stouter appearance than normal branches. Lateral buds were not as common on these branches as on normal ones, but terminal buds were always well developed.

Brooms of Non-parasitic Origin on Conifers in General

A similar broom occurs on a variety of other conifers, and it is perhaps relevant to mention these here. The following list is a guide to coniferous brooms which have been referred to in the literature and which are considered of non-parasitic origin therein.

Abies alba Mill.	(Tubeuf 1933)
Larix decidua Mill.	(Tubeuf 1933)
Picea abies (L.) Karst.	(Tubeuf 1933)
Pinus mugo Turra	(Tubeuf 1910b, 1912b, 1933)
Pinus strobus L.	(Badoux 1898, Koltz 1898, Tubeuf 1905b, 1933)
Pinus sylvestris L.	(Witmack 1868, Hoffmann 1871, Zang 1905, Tubeuf 1905a, 1910a, 1933, Müller 1908, Zach 1911, Hintikka 1933, Liese 1933, 1935)
Pseudotsuga menziesii (Mirb.) Franco	(Coheen *et al.*, 1951)
Taxodium distichum (L.) Rich.	(Muth 1904)

Reports from Alberta and British Columbia

A general interest in hypertrophy led to the examination of various types of coniferous brooms in the two western provinces during the last three years. The following list of observations excludes brooms where pathogens were the obvious cause (rust- and dwarf mistletoe brooms). In all cases listed, evidence of pathogenic organisms could not be found in the field. While it is true that not all of these instances could be checked from nearby because of inaccessibility, familiarity with these brooms makes recording them seem justifiable.

Larix laricina (Du Roi) K. Koch	Ca. 40 mi. south of Lesser Slave Lake, Alberta.
Larix lyallii Parl.	Halfway Cabin above Mt. Temple lodge, Banff, Alberta.
Larix occidentalis Nutt.	1. Kimberley, B. C. (entire tree broomed; Fig. 5) 2. Kimberley, B. C. (large broom; Fig. 6)
Picea glauca (Moench) Voss	Seebe, Alberta.
Pinus contorta Dougl. ex Loud.	Waterton Lakes Park, Alberta.
Pseudotsuga menziesii (Mirb.) Franco	See distribution map, Fig. 8, and Figs. 1-4.
Taxus brevifolia Nutt.	Cadboro Bay, Vancouver Island, B. C.
Thuja plicata Donn ex D. Don	Massett, Q. C. I., B. C.

Causes Suggested

Two possible causes have been suggested in the literature for this type of brooming on conifers. Conclusive evidence for either, however, has not been presented.

Zach (1911) is the only worker claim-

ing a parasitic cause for the broom on *Pinus sylvestris*. He concluded that the broom on this pine is to be regarded as a diseased condition of the buds, the pathogen being a *Strepthrix*-like organism. Recession of growth due to the presence of this organism would result in the short and dense growth of the broom. The evidence presented for this view, however, is not convincing. The "diseased buds" were not compared with healthy ones; the variety of cultured organisms strongly suggests impurities; and there are indications that normal anatomical processes in the developing pine shoot were misinterpreted or given unwarranted significance.

Much more reasonable, though not definitely established, is the view that this type of broom is due to a somatic mutation and subsequent divisions of the abnormal mutant cell. Tubeuf (1933) as well as Liese (1933) and Hintikka (1933) were able to demonstrate that at least some progeny of the brooms retained the abnormal characteristics to some degree. However, no controlled pollination or cytogenetical studies were conducted and until this is done, no convincing conclusions can be drawn. Nevertheless, the observations of these workers serve as a strong indication of a genetical rather than a parasitic cause. If this view proves correct, we can regard conifers bearing this type of broom as chimaeras in the sense of Neilson Jones (1934; see pp. 1-2): "any plant . . . built up of genotypically different tissues however the composite structure may have arisen."

Anatomical Work and Results

Microscopical preparations were made of broomed Douglas-fir material from seven different collections, six of which were from Lasqueti Island, B. C., and one from Seebe, Alberta. In addition, a few slides of healthy material were made for comparison. Of all material sectioned, only one branch showed a mycelium within living tissues. In this material the mycelium ramified through the cortex as well as the pith region. No fructifications were encountered. Because of the absence of mycelium in living tissues of all other branches examined, it must be assumed that this fungus is accidental or secondary; in any case, it can not be the sole cause of brooming. The only other mycelium seen in the preparations is strictly superficial and does not enter living tissues. Since some saprophytic mycelium is found on almost all branches in nature, it would be unreasonable to ascribe to it alone the ability to induce brooms.

It seems a fair generalization to say that no mycelium is present in living tissues on this broom on Douglas-fir. In other words, a fungus does not seem to be the cause of this malformation. This conclusion is in line with the work of Coheen *et al.* (1951), who were unable to isolate a causal organism. Limited attempts at isolation at the University of British Columbia were similarly fruitless.

The striking differences between brooms and normal branches seem to disappear when the same material is observed under the microscope. In fact, no abnormality whatsoever could be detected in the gross anatomy of broomed branches. The organization of tissues, frequency of cell types, and relative proportions of the tissue regions seem to be basically the same as those of healthy material. This negative evidence again points to the chimaeral hypothesis.

Silvicultural Significance of Non-Pathogenic Brooming of Conifers

The fact that entirely broomed individuals can arise as progeny of brooms has been clearly shown by Tubeuf (1933), Liese (1933), and Hintikka (1933). Liese also found a completely broomed individual established in nature. The specimen of *Larix occidentalis* near Kimberly, B. C., may be another case in point (Fig. 7). The question therefore arises whether any silvicultural significance is to be attached to this type of brooming.

It seems reasonable to expect that in

nature this kind of broomed progeny would quickly perish if any competition is operative. The rarity of cones on brooms would probably apply also to entirely broomed trees, and places these at a reproductive disadvantage. Hintikka (1933) believed the mortality of broomed seedlings to be higher than normal. The reduced growth rate is perhaps the most obvious competitive disadvantage. Liese (1933), however, also considers the root system of the broomed progeny to be inferior to that of healthy comparable seedlings. Both the rarity of occurrence and these observations, therefore, point to silvicultural insignificance.

Possible Future Work

The possibilities of future work on this problem are threefold. First of all, a brief anatomical study of the unexplained brooms on other conifers should be made. In the case of Douglas-fir, the evidence is fairly convincing that no fungus organism is consistently associated with the brooms. The other coniferous brooms listed should also be studied in this regard.

Secondly, wherever pathogens are clearly absent, controlled pollination work between brooms mutually and between brooms and normal branches will be able to establish whether or not a mutation is the cause of brooming. The nature of the progeny may then give some hint as to what kind of genetical change is involved. This breeding work will be difficult because of the rarity of brooms, and especially of cones on these brooms. However, results of this type would be of great value in understanding the problem. Additionally, this work may yield valuable information for horticultural purposes, since dwarfed trees are prized objects.

The most difficult, but perhaps also the most reliable approach would be a cytogenetical study. The demonstration of the actual genetic basis of this malformation is further complicated by the rarity of male and female cones on these brooms, and this may necessitate work on the apical meristem of shoots instead. It is nevertheless possible that a more thorough search would reveal production of some cones on certain brooms, and in this case the work of Zenke (1953) on meiosis of Douglas-fir forms a convenient starting point for a cytogenetical study.

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Growth Habits of the Eucalypts

The paper *Growth Habits of the Eucalypts* by M. R. Jacobs reviewed by John W. Duffield in FOREST SCIENCE 3:60, may be purchased from the Director General, Forestry and Timber Bureau, Canberra, Australia for 30/-(A) including postage.

Possible Occurrence of Viable Unfertilzed Seeds in Douglas-fir

BY
A. L. ORR-EWING

THE DEVELOPMENT of unpollinated cones with fully formed but empty seed is known as parthenocarpy and according to Hummel (1930) was first investigated in the gymnosperms by Kurdiani. He found that parthenocarpy was of common occurrence in *Abies, Juniperus, Larix, Picea, Taxus* and *Thuja* whereas Syrach Larsen (1937) later reported it in *Chamaecyparis, Cryptomeria, Pseudotsuga* and *Tsuga*. Parthenocarpy in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), therefore, is of normal occurrence and has already been reported by Allen (1942). The seeds in such cones are fully formed and of normal appearance but they are usually empty. Allen (1942), however, obtained three viable seeds from the parthenocarpic cones of two trees, the cones being isolated with bags one week before emergence from the bud scales. The possibility of some pollen contamination can not be entirely discounted but the results were still of considerable interest. Reproduction without normal fertilization by a male sperm is known as apomixis, and Gustafsson (1946) has divided this phenomenon into two groups, reproduction by vegetative means and reproduction by seeds. This latter group is known as agamospermy and Stebbins (1950) has pointed out that its simplest form is adventitious embryony in which the embryos develop directly from the diploid sporophyte tissue, omitting the gametophyte stage completely. Plants produced by this means would have the identical inherent characteristics of the parent. Stebbins has added that the more common methods of agamospermy include a complete sporophyte-gametophyte-sporophyte cycle of alternation of generations, but a cycle in which diploid embryos arise as a result of some method of circumventing meiosis. Plants produced by this method may or may not be identical in genotype with the parent and could be rather variable. This very brief description of agamospermy may serve to emphasize the extreme complexity of this method of reproduction which, however, has been described in detail for some of the angiosperms. Its occurrence in the gymnosperms has not yet been confirmed. Agamospermy, however, could be of the greatest value to the forest geneticist, and an attempt was recently made to corroborate Allen's (1942) earlier results with *Pseudotsuga menziesii*.

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Results

In 1952 and 1954, controlled pollination studies were made with this species in the course of another study[1], and it was a comparatively easy matter to isolate some cones and to leave them unpollinated. In 1952, cones on two trees were isolated with viscose-casing bags two weeks before they had emerged from the bud scales so that there would be little opportunity for any pollen contamination. The cones were collected in the fall and the seed extracted. The results of the germination test conducted on the seed showed that 22 seeds from the 11 cones of Tree No. 2 contained embryos (Orr-Ewing, 1954). Twelve of these seeds germinated and the seedlings were all examined and found to be diploid. Next, they were carefully planted out but they were not particularly vigorous, and only seven had survived at the end of the growing season in 1956. Although these seedlings had to be carefully transplanted to different locations in 1953, 1954, 1955 and 1956, they still show remarkably little variation in either height or form. Their range in height growth is shown in Table 1 and can be compared directly with that of pollinated seedlings of the same age from the same parent tree. These latter seedlings have resulted from either wind-, self-, or cross-pollination and have been grown under comparable conditions and transplanted the same number of times. The number of seedlings from the parthenocarpic cones is admittedly small when compared with the others but their range of heights expressed as a percentage of the mean is considerably less. In spite of disturbance caused by transplanting, the uniformity of these seedlings is striking. Figures 1 and 2 show two of them at the end of the growing season in 1956. Such uniformity certainly suggests that agamospermy may have occurred.

[1]Orr-Ewing, A. L., 1956. An investigation into the effects of self-pollination on *Pseudotsuga menziesii* (Mirb.) Franco. Diss., Univ. of B. C., Vancouver.

Since the possibility of some pollen contamination can not be entirely discounted, a check was made to see whether it might have occurred. One of the parthenocarpic cones which had been isolated on the same tree was removed a week before fertilization would have normally occurred and the 48 ovules were killed, fixed, and embedded. Sections of these ovules, however, revealed no trace of either pollen grains or pollen tubes.

There was, unfortunately, no opportunity of obtaining direct cytological evidence of agamospermy in Tree 2 as there were no cone crops the following years. Further controlled pollinations, however, were made on other trees in 1954 and some of the isolated cones were again left unpollinated on five of these trees. Sample cones were then removed at regular intervals from each tree and the ovules killed, fixed, and embedded. Forty-one of these ovules from four of the trees have been sectioned at the present time but none of the sections has given any indication of the manner in which agamospermy might conceivably develop. This was particularly unfortunate as two embryos were found in the ovules of cones sampled from two of the trees at the end of July. The barren ovules of the parthenocarpic cones usually collapsed three to four weeks after the date that fertilization would have normally occurred, and the finding of these two sound ovules was most unusual. Both of the embryos were found to be diploid and one of them is illustrated in Figure 3.

The possibility of pollen contamination was again considered remote as the cones in which these embryos were found were isolated at least two weeks before their emergence from the bud scales. Pollen dispersion from both of the parent trees, moreover, did not begin until five weeks after isolation. The viscose casing bags were removed only when the scales on these cones had completely sealed and the cones themselves had started to invert. These

TABLE 1. Range in height growth of progeny from Tree 2, 1956.

Pollination	No. of seedlings	Range in inches	Mean height in feet	Range as percent of mean
None	7	13.5-25.0	17.3	66
Wind	37	12.4-45.8	27.4	122
Self	33	4.5-38.2	18.8	179
Cross	55	15.7-44.8	33.1	88

bags have been found very effective in screening cones from pollen as there was no sign of either pollen grains or pollen tubes in any of the sections of the ovules from these cones. Nienstaedt and Kriebel (1955) have also tested bags of the same same material and have found them satisfactory in preventing pollen penetration.

In the fall, the remaining parthenocarpic cones were removed from the five trees and the seed extracted and cleaned. The results in Table 2 showed that very few cleaned seeds remained and that none of these contained embryos.

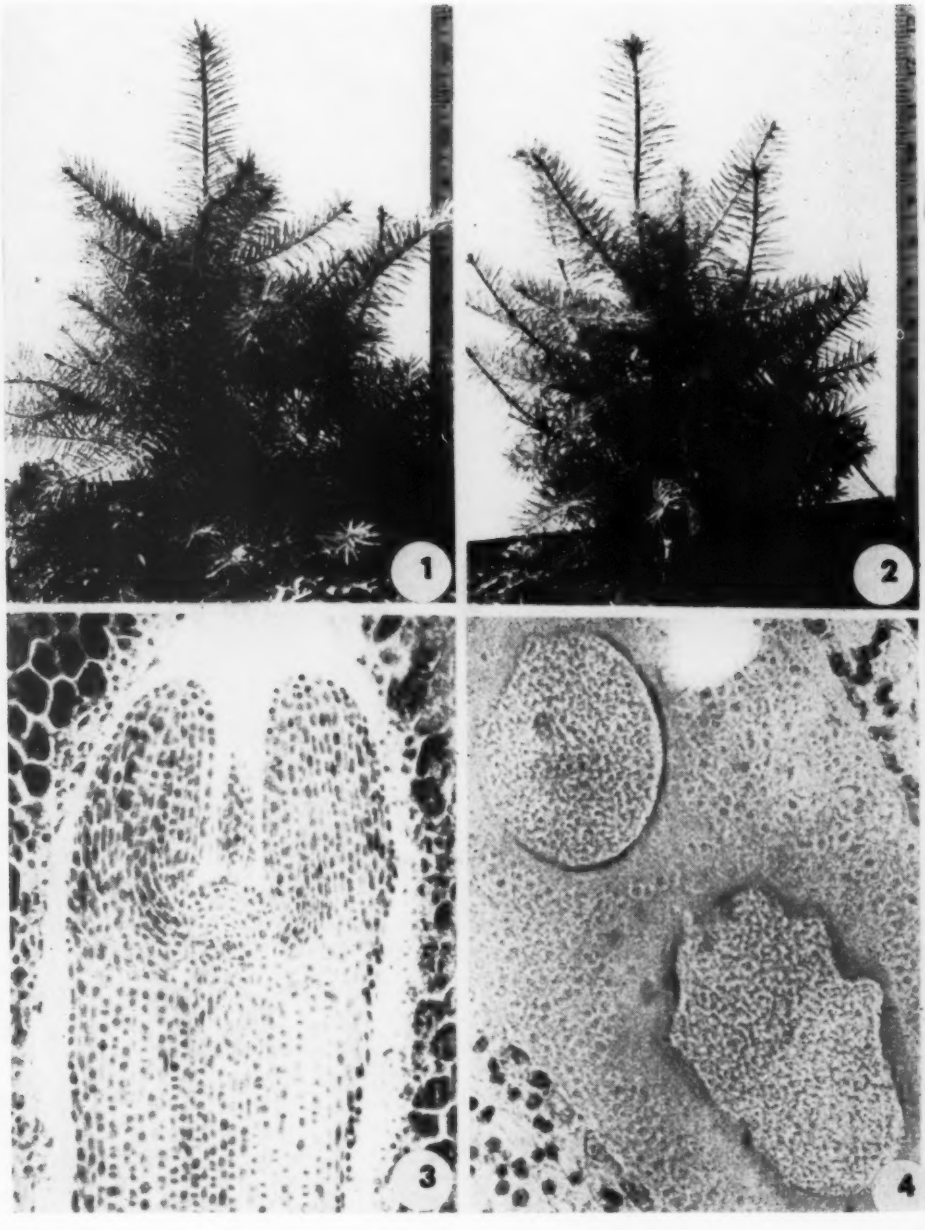
Discussion

The evidence to date suggests that agamospermy may be of rare occurrence in Douglas-fir and that positive evidence of the methods by which it may develop will be difficult to obtain. The striking uniformity of the seven seedlings from Tree 2 is perhaps suggestive of adventitious embryony. Another possible manner by which agamospermy could conceivably occur was suggested by an examination of some sections of a barren ovule from a cone of Tree 1 on which controlled pollinations had been made in 1952. This cone had been self-pollinated and removed at the time that fertilization would be normally expected. Sections of the ovule, however, showed none of the familiar stages of either pollen development or fertilization. On the other hand, one of the sections, illustrated in Figure 4, shows an enlarged nucleus in close proximity to that of the egg. The sperm nucleus of Douglas-fir and its union with the egg nucleus has been observed in numerous sections and it is much the smaller of the two nuclei. It is, therefore, most unlikely to be the second nucleus shown in the section.

There are two possible explanations, the one being that the original egg nucleus has divided and that these two nuclei are the result of this division. Saxton's (1909) investigation with *Pinus pinaster* is of interest in this particular connection as he reported that in one section of an ovule the egg nucleus had begun to divide before the pollen tube had reached the archegonium. The other explanation for the two nuclei shown in Figure 4 is that one

TABLE 2. Germination test on the seed from parthenocarpic cones.

Tree no.	No. of cones	No. of seeds	No. of cleaned seeds	No. of seeds germin.	No. of seeds with embryos
4	38	1419	2	0	0
7	35	966	7	0	0
8	53	2368	9	0	0
9	30	1821	0	0	0
10	56	2719	5	0	0



FIGURES 1 and 2. *Two of the four-year old seedlings originating from the parthenocarpic cones of tree 2.* FIGURE 3. *One of the embryos found in a parthenocarpic cone. Tree 4 (X105).* FIGURE 4. *The two nuclei in the archegonium of a barren ovule. Tree 1 (X395).*

is an enlarged ventral canal cell nucleus which has broken through the cell wall. This would appear to be the more likely explanation as there was no sign of this nucleus in the other series of sections from the ovule. Allen (1943), moreover, has earlier reported that the ventral canal cell nucleus of this same species may very rarely escape from its cell wall and enlarge considerably. It is conceivable that union of the ventral cell nucleus with that of the egg could actually occur.

This is by no means the first occasion in the gymnosperms that such a union has been suggested. Chamberlain (1935) declared that the first two cases of fertilization described for conifers were abnormal, as Strasburger in 1878 described two gamete nuclei of about equal size in *Picea vulgaris*. Coulter nearly 20 years later described two fusing gametes of about equal size in *Pinus laricio*. Chamberlain added that there was little doubt that the sperm nucleus in both cases was an enlarged ventral canal cell nucleus and that his own work with *Pinus* made this interpretation practically a certainty. Hutchinson (1915) reported that in *Abies balsamea* the ventral canal cell nucleus occasionally broke through the cell wall and moved towards the egg nucleus. Johansen (1950) has referred to an early report with *Ginko* where fusion of the ventral canal nucleus with that of the archegonium has been described. He added that it was not known whether this could result in the development of a normal embyro but that it was not beyond the realm of possibility. Sedgwick (1924) declared that fertilization in *Encephalartos* was not observed and that fertilization by a sperm was apparently not necessary for the successful development of embyros. He found that in both greenhouse and field material the ventral canal cell nucleus instead of degenerating, enlarged and was seen approaching the egg. Sedgwick also presented additional cytological evidence to support his claim that embyros could be produced without pollination taking place. His evidence is corroborated by that of Chamberlain who added that embyros of this genus were found in conservatory material where no male cones were present.

Such varied reports admittedly present no conclusive evidence that embyros could be produced by these means but they do suggest that agamospermy may occasionally occur. Further cytological studies of ovules which have been isolated from pollen contamination would appear very worth while. These past reports also emphasize the lack of information which still exists on the crucial aspects of reproduction in the commercially important gymnosperms. Johansen (1950), for example, has stated that the process of syngamy has been accurately described in its entirety for only a few species in the *Pinaceae*, and that the most comprehensive account is for two species in the genus *Pinus*. It might be added that this same family includes such important genera as *Picea*, *Abies*, *Pseudotsuga*, *Tsuga* and *Larix*.

Summary

A few viable seeds were germinated from the parthenocarpic cones of one Douglas fir (*Pseudotsuga menziesii*) in 1952 and the surviving seedlings have shown little variation in either height or form. Two embryos were later found in the ovules from the parthenocarpic cones of two other trees. The seedlings and embryos were found to be diploid. No conclusive cytological evidence of the origin of agamospermy was obtained but the possibility of pollen contamination is considered remote. Some of the possible methods by which agamospermy could occasionally occur in this species are briefly discussed.

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Errata

In the article *Studies of Regeneration in Forest Stands Devasted by the Spruce Budworm* by A. W. Ghent, D. A. Fraser and J. B. Thomas (FOREST SCIENCE 3:184-208) the following line should be inserted on p. 201, column 2, after line 22: "tailed probability of .03. Although".

Hail Damage to Five-year-old Red Pine in Northern Wisconsin

BY
DANIEL M. BENJAMIN

THE ESTABLISHMENT and growing of trees for forest products is an undertaking fraught with many hazards. Weather, fire, disease and insects all take their toll and all tree species are susceptible to injury. Among the factors causing damage in young plantations, insects play the most important role. More trees are killed, stunted or deformed by these pests than by other factors, including fires.

Because of the frequency with which new plantings are damaged by insects, the presence of dead or discolored twigs is generally considered sufficient evidence that some pest is at work. In some instances, however, examination shows that though the pest is present, its numbers are insufficient to cause the loss observed. The damage, therefore, must be attributable to some other factor. A striking example of the gross similarity between insect damage and that caused by meteorological phenomena occurred in northern Wisconsin in 1955 when a severe hail storm swept a young red pine plantation, which was lightly infested by the Saratoga spittlebug, *Aphrophora saratogensis* (Fitch).

On May 3, 1955 a severe squall line passed through Wisconsin, and from about Viroqua northeast to Eagle River, violent storms occurred at several points. Considerable property loss resulted from the wind, lightning, rain and hail. Tree growth had just begun in the northern part of the state and newly-expanded buds and succulent twigs were unable to withstand the bombardment of hailstones—some of which were reported to be the size of "golf balls" and "walnuts." One of the areas most severely hit by the hail was at Starks, where barn roofs were punctured and windows were broken. Directly in the path of the hail storm was a five-year-old red pine (*Pinus resinosa* Ait.) plantation averaging about 30 inches in height. The damage caused by the hail was exceedingly severe, and the similarity to injury caused by the Saratoga spittlebug most striking. Twig mortality became evident in late June as the needle-bearing branches of the previous two years dried and the needles turned reddish brown. At first sight from a distance, and in light of previous experience, a diagnosis of Saratoga spittlebug injury was made. It was not until the injured red pine saplings were examined closely that the cause of the damage was determined.

This plantation was found also to be lightly infested by the Saratoga spittlebug. Since the gross characteristics of the damage appear so similar from a distance it seems worthwhile to record the similarities and differences between the two types of damage (Table 1).

Approved for publication by the Director of the Wisconsin Agricultural Experiment Station. The author is Associate Professor, Department of Entomology, University of Wisconsin, Madison 6, Wis.

TABLE 1. Similarities and differences between damage to red pine by Saratoga spittlebug and hail.

Characteristics of injury to red pine by the Saratoga spittlebug:	Characteristics of hail injury to red pine:
Stunted lateral and terminal twigs.	Normal elongation of lateral and terminal twigs.
Dead twigs with brown needles intact, or denuded twigs, distributed at random over upper half of crown.	Dead twigs with brown needles intact, or denuded twigs, in general restricted to one side of tree (Figure 1) and distributed over entire crown vertically, or most commonly in upper crown.
Dead trees located in groups or pockets.	Dead trees distributed uniformly or in swath through plantation.
Terminal and lateral buds intact.	Terminal and lateral bugs missing on many twigs.
Feeding punctures and associated resin infiltration pockets in outer layers of wood and inner layers of phloem numerous and coalesced on dead twigs.	Feeding punctures, if present, not numerous or coalescing.
Occurrence of damaged trees associated with ground cover preferred by nymphal spittlebugs.	Damaged trees not associated with any ground cover distribution pattern.
External bark lesions absent.	External bark lesions and debarked areas common, restricted to upper and windward sides of branches. (Figure 2)
Damage restricted to red and jack pine.	Damage to both coniferous and deciduous trees common.

By employing these criteria, it was relatively simple to distinguish between hail injury and spittlebug damage.

Numerous accounts of destruction of forest stands by hail have appeared in forestry literature. Most frequently, damage to specific tree species is cited, and mortality and subsequent recovery are described only in general terms (Basham, 1953; Riley, 1953; and Thomas, 1956). Seldom is detailed information concerning the magnitude of the loss presented, probably because of the variation in the intensity of the hail bombardment and resulting tree injury throughout the path of the storm. The Starks plantation presented an excellent opportunity to obtain more precise information on the intensity of damage in a localized area.

This plantation was established in 1950 by machine planting at approximately 6 x 6 foot spacing on gently rolling terrain adjacent to open areas used for potato farming. Extending in an east-west direction, it covered an area three-eighths of a mile long by 360 feet deep. The hail storm swept through the entire planted area, passing from southwest to northeast. By mid-June, dead and discolored branches and twigs were evident throughout the area.

FIGURE 1. *Red pine damaged by hail in Wisconsin on May 5, 1955. (Photo July 1956)*

FIGURE 2. *Red pine debarked by hail on May 5, 1955. (Photo July 1956)*

On July 15, 1955, 10 sample plots of 10 trees each were established at random to evaluate the magnitude of the damage. The height of each tree was recorded together with information concerning the number and age of living and dead twigs and branches at each whorl and the presence or absence of current shoot elongation. Notes were made of infestation by bark and wound-feeding insects.

Tree mortality resulting from the hail bombardment averaged four percent and was confined, in general, to the smaller trees. The average height of killed trees was 22 inches, with a range from 12 to 36 inches, while surviving trees averaged 36 inches and ranged from 20 to 56 inches. Among the survivors, 78 percent had the leader or terminal bud destroyed; 33 percent also had the 1954 terminal growth destroyed.

Hail injury was most severe on the side of the trees facing the bombardment, with twig mortality averaging 50 percent on the south quadrant and only 19 percent on the north quadrant. Mortality of 1955 lateral buds surrounding the terminal bud of the leader averaged 65 percent; 66 percent of the current lateral buds over the remainder of the crown failed to elongate. In addition, 33 percent of the lateral growth of the 1954 season was killed. Apparently no additional twig or tree mortality occurred during 1956.

During the latter part of 1955, wounds on approximately five percent of the surviving trees became infested with undetermined lepidopterous and coleopterous larvae. This infestation has since subsided and the recovery of the damaged trees appears well under way.

It is evident that the damage to this planting of small red pines was severe. Surviving trees will be misshapen for several years although it is anticipated that permanent injury will be evident as crooking only in the first few feet of the bole.

Summary

Within the Lake States, where Saratoga spittlebug damage is common, twig and branch mortality on red pine reproduction is often due to this pest. Injury caused by hail bombardment of a five-year-old red pine planting near Starks, Wisconsin, is contrasted with spittlebug damage, and the intensity of bud and twig mortality assessed. Tree mortality was four percent. Terminal bud mortality average 78 percent and lateral bud mortality 65 percent. Terminal elongation for the year preceding the storm was destroyed on 33 percent of the trees and lateral twig mortality averaged 66 per-

cent. Wound infestation by unidentified insects occurred on five percent of the trees, and as the trees recovered these infestations subsided.

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Tables for Use with Binomial Samples—Contingency Tests, Confidence Limits and Sample Size Estimates

By Donald Mainland, Lee Herrera and Marion I. Sutcliffe. Dept. of Medical Statistics, New York University. 83 pp. (Photo-offset). 1956. $2.00.

Statistical tables published by Mainland and his collaborators during the past eight years (Can. J. Research, E, 26:1, 1948; Science, 116: 591, 1952; Can. J. Med. Sci., 31: 406, 1953) have been in demand, not only in medicine for which they were originally intended, but also in agriculture and other fields. Since reprints of the first two publications are exhausted, all the tables, with instructions are now re-issued in book form. The tables not only remove the need for computation or reduce it to a line or two of simple arithmetic. They provide much more accurate answers than can be obtained by the approximate methods commonly used, such as the chi-square test and the standard error of the binomial. All the tables deal with qualitative data (of the A, not— A type), such as deaths and survivals, percentages of defective products, and all-or-none responses; but they have also many uses in the treatment of measurement data without the assumption of the normal curve or other continuous distributions. The tables comprise three groups: (1) Tables I-IV are for the significance testing of fourfold contingency tables. For samples up to size 20, exact probabilities are given. For equal samples up to size 500, differences required to give significance at the 5 per cent and 1 per cent levels are tabulated, and these tables can be used also in many problems involving unequal samples. (2) Tables V-IX show binomial confidence limits for sample sizes from 1 to 100,000, with intervals of 1 per cent or less between sample percentages for the 95 per cent and 99 per cent limits, and somewhat wider intervals for the 80 per cent limits. (3) Estimates of sample sizes required under various conditions are obtainable from all the tables, but Table X is specially designed for this. With sample sizes up to 100, it shows the probability of an experiment being "successful" in the sense of producing a significant difference between observed sample frequencies when there is, in fact, a difference in population frequencies.

Two Natural Iowa Hybrid Poplars

BY
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KENNETH A. BRINKMAN
A. L. McCOMB

DISCOVERY of two stands or clones of aspen-poplar hybrids in Van Buren County, southeastern Iowa, has attracted considerable attention because of increasing interest in fast-growing hybrid poplars for veneers and pulpwood. English names and botanical descriptions of these new hybrids are recorded here.

These clones are named Shimek poplar and Sherrill poplar. They have been identified as natural hybrids (first generation or F_1) between white poplar (*Populus alba* L.), which was introduced from Europe and Asia, and bigtooth aspen (*P. grandidentata* Michx.), native but at the southwestern border of its range. It is not known which species was the female parent and which the male, but most white poplars in the United States are female. All crosses with this parentage may be designated by the formula *Populus alba* × *grandidentata*. Shimek poplar is female and has good stem form; Sherrill poplar is male, has average form, and has wood with an attractive wavy figure, suitable for veneeers and wall paneling. Both are readily propagated from stem and root cuttings under favorable conditions, although less easily in field planting, and grow rapidly.

The dates of origin of these two hybrid poplars are unknown. The Sherrill stand apparently is somewhat older than the present Shimek stand. Obviously, white poplar could not have been introduced prior to settlement of this area, approximately 120 years ago. The area in which the Shimek stand is located was cleared and grazed by sheep until 1900. Because species of *Populus* have exacting seedbed requirements, this hybrid probably originated soon after grazing ceased, between 1900 and 1910 or later. Afterwards the area became covered with oak timber, which was clear cut in the early or mid 1920's for mine props. No cutting has taken place since then.

Apparently the trees at each locality originated by root sprouts from a single hybrid seedling. The presence of flowers of a single sex in each stand, though not proof, suggests origin from one seedling rather than more.

Other Studies of *Populus alba* × *grandidentata*

Populus alba of Europe and Asia and *P. grandidentata* of northeastern United States and southeastern Canada are both in *Populus* section *Populus* (*Leuce* Duby) which contains the white poplars and aspens. The species within this section cross readily, and natural and artificial hybrids between these two closely related species have been reported by various investigators.

Canadian studies of natural and artificial hybrids between *P. alba* and *P. grandidentata* were summarized by Farrar (1947) and reviewed by Pauley (1949). Heim-

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burger (1936, 1940) discovered several hybrid trees in 1935 and the next year made this cross artificially. These clones maintained hybrid vigor and were resistant to disease. Identical juvenile shoots of the wild trees and artificially produced clones confirmed the hybrid origin of the former. He observed that the parent species usually flowered about the same time in nature, while *P. tremuloides* Michx. usually blossomed a week to 10 days earlier.

Peto (1938) listed 13 of these natural hybrid trees of *Populus alba* × *grandidentata* from Ontario and Quebec. In cytological examinations he determined the chromosome numbers of hybrids and parents as $2n = 38$. He also found triploids of *P. alba*, with 57 chromosomes. He noted that this hybrid resembled *P.* × *canescens* but was distinguishable by leaf shape.

From studies of the F_1 and F_2 generations at 5 years of age, Johnson (1946) found that the F_1 showed hybrid vigor and was taller than parents and the F_2 was shorter than parents. The high rooting capacity of *P. alba* was transmitted as a dominant character, and for the variations in leaf characters different modes of inheritance were assumed. In experiments on relation of growth rate to wood quality in hybrids of *P. alba* with *P. grandidentata* and *P. tremuloides*, Johnson (1942) found nothing to indicate that rapid growth is seriously detrimental to wood quality.

By 1945 Johnson and Heimburger (1946) had made additional crosses, including hybrids of *Populus alba* × *grandidentata* with other poplars. Later Heimburger (1954) reported on progress of these Canadian hybrid poplars. In 1954, 5 clones of *P. alba* × *grandidentata* were listed.

Naming the Hybrid Clones

A uniform simple nomenclature is desirable for the numerous clones in the genus *Populus*. These vegetatively propagated variations, easily produced by hybridization, correspond to a single plant. Under the International Code of Botanical Nomenclature, a hybrid between two species is designated by a formula and, whenever it seems useful or necessary, by a name. For example, all natural and artificial hybrids between variations of the same two parent species would bear the same binomial, although the different clones would be propagated vegetatively and maintained as distinct.

Stout (1929), Stout and Schreiner (1933), and Pauley (1949), among others have pointed out the confusion associated with binomials for hybrids and clones in this genus. Schreiner and Stout (1934) set a desirable precedent in assigning special horticultural names, such as Geneva poplar and Oxford poplar, to 10 of their most promising hybrids. These English names were accompanied by scientific names of the parents and by English botanical descriptions. Pauley (1949) recommended the adoption of individual names or numbers for these vegetatively propagated poplars, regardless of their taxonomic status.

The International Code of Nomenclature for Cultivated Plants (Stearn, 1953) provides for common names of cultivated varieties, including clones. Application of this Code to the genus *Populus* is the subject of reports by the International Poplar Commission, Food and Agriculture Organization (1955, 1956). It was suggested that this Commission register names of cultivated poplars, mostly clones, under common names such as the following: Poplar 'italica,' Poplar 'Carolin,' and Poplar 'robusta.' Thus, common names are adequate.

Apparently the hybrid between *P. alba* and *P. grandidentata* has not been given a formal Latin binary name. It seems neither useful nor necessary at this time to assign to these hybrids in Iowa a binomial that would include all other natural and artificial hybrids between the same parent species. Moreover, these Iowa hybrids are restricted in natural occurrence to two clones occupying only a few acres.

Shimek Poplar

Location and Description of Stand

McComb and Hansen (1954) studied this clone, publishing a photograph of the trees and a stand and stock table based on a 1/10-acre sample. The present stand of about 2 acres is located on Shimek State Forest, about ¼ mile northwest of the headquarters area and nearest house, in NE ¼, NW ¼, Sec. 36, T. 68 N., R. 8 W., approximately 1½ miles east of Farmington, Iowa. The trees apparently are a clone established vegetatively in an open area by root sprouts from one original seedling. They now form a heavily stocked stand spreading on a west-facing 28 percent slope on the lowest third of a sloping ridge along a small valley.

In the summer of 1947 this stand was brought to the attention of Iowa foresters by the late Robley McIntosh of the State Conservation Commission and supervisor of Shimek State Forest at that time. He and John Wakefield, former Superintendent of State Forests in Iowa, inspected the stand and considered it to be aspen, probably bigtooth aspen. When making a type map of the area in the winter of 1946-47, foresters from the Ames Forest Research Center classified the stand merely as aspen. In 1952 during a search for bigtooth aspen, McComb examined this stand. Botanical specimens were sent to Scott S. Pauley, then at Harvard University, who confirmed the identification as a hybrid between *Populus alba* and *P. grandidentata*, having produced the same hybrid artificially by controlled pollination.

The present Shimek stand apparently originated from prolific root sprouting after removal of the original trees or stand. This stand is heavily stocked, much more so than the Sherrill stand. Competition has killed many trees. The average age of the dominant trees of the Shimek clone was at least 26 years in 1954. The largest tree, growing under very favorable conditions, was 99 feet high and 15 inches d.b.h. Three trees cut in 1954 were 28, 26, and 25 years old at the stump and 12.3, 8.7, and 8.4 inches d.b.h., respectively. On a 1/10-acre plot in the center of the clone, measured by McComb and Hansen (1954) in 1952, the trees ranged from 3 to 9 inches d.b.h. and from 34 to 74 feet in height (Fig. 1).

Botanical Description

The name Shimek poplar identifies this clone with the Shimek State Forest, within which it occurs naturally. Also, it fittingly honors Dr. Bohumil Shimek (1861-1937), Professor of Botany at the University of Iowa and author of various publications on the plants of Iowa.

Shimek poplar or Poplar 'Shimek,' a new natural hybrid clone (female) between

FIGURE 1. *Shimek poplars on the Shimek State Forest, east of Farmington, Iowa. (Forestry Department, Iowa State College, photo.)*

white poplar and bigtooth aspen (*Populus alba* × *grandidentata*), intermediate between the parents. Tall, rapidly growing tree in a heavily stocked, 2-acre stand at least 26 years old, 10-23 m. (34-74 feet) tall and 8-23 cm. (3-9 inches) d.b.h., maximum 30 m. (99 feet) tall and 38 cm. (15 inches) d.b.h., trunk straight and slender. Bark light greenish gray, smooth, about 0.5 cm. thick, toward base of larger trunks developing diamond-shaped cracks 0.5-2.5 cm. long, and at base becoming rough and furrowed and gray and thicker, the inner bark light yellow and bitter. Wood whitish, soft. Twigs gray, brownish near tip, densely white puberulent when young, becoming glabrous. Winter buds narrowly ovoid, acuminate, mostly 5-8 mm. long but flower buds mostly 10-12 mm. long, gray, the dull brown bud scales finely gray appressed puberulent.

Petioles 2-6 cm. long, flattened, densely white puberulent when young, becoming glabrous. Blades ovate, longer than broad, 4-8 cm. long, 2.5-6 cm. broad, truncate at base and acute at apex, the margins coarsely dentate with 4-8 mostly large acute teeth on each side and often with 2 round glands (sometimes 1 or none) on upper surface at base of blade, lateral veins mostly 4-5 on each side including 1 pair at base and at an angle of about 45° from midrib, at maturity glabrous or nearly so on upper surface except near base and the paler lower surface also nearly glabrous except for minute pubescence chiefly along midrib and lateral veins. Very young leaves white puberulent on upper surface and white tomentose on lower surface. Sprout leaves larger and becoming relatively broader, the nearly terete, white tomentose petioles 2-8 cm. long, the blades becoming 8-15 cm. long and 6-15 cm. broad, subcordate at base and acute to acuminate at apex, the margins irregularly serrate with unequal teeth and sometimes slightly 3- or 5-lobed, the upper surface green and becoming nearly glabrous, and the lower surface white tomentose.

Flowering catkins female, about 3-5 cm. long and 4-7 mm. in diameter, drooping, with light green pubescent axis, many-flowered, appearing brown because of the prominent brown bracts. As base of each flower is a membranous light brown bract or scale 3-4 mm. long and 1-1.5 mm wide, spatulate to elliptic, the apical part irregularly dentate with short teeth less than 0.5 mm. long and fringed with long hairs (Fig. 2). Individual female flowers 3-4 mm. long, the light green cup-shaped basal disk 1-2 mm. long including the narrow short pubescent stalk and conical cup slightly pubescent toward base, margin slightly wavy and only slightly oblique, covering less than half the height of the ovary; pistil 2-carpellate; ovary green, ovoid, 2 mm. long and less than 1 mm. in diameter, containing 4-6 ovules attached near base on 2 parietal placentas; stigmas 2, each 2-forked near base, whitish and slightly fleshy, the 4 linear flattened forks spreading and becoming 1 mm. long, afterwards drying, turning brown, and shedding.

Fruiting catkins 5-10 cm. long, slender, the ovoid green capsules 3 mm. long, minutely tubercled, splitting into 2 valves, with brownish remains of cup 0.5 mm. long at base, filled with tufts of white hairs (coma) but seeds not developed.

Sherrill Poplar

Location and Description of Stand

This stand, larger than 2 acres, is also located in Van Buren County, about 10 miles west northwest of the Shimek stand and on State highway 2, about 5½ miles southeast of Keosauqua, Iowa. Most of it is on the John Sherrill farm in NW ¼, SW ¼, Sec. 21, T. 68 N., R. 9 W., in a forest on a north-facing slope of a small valley. A few trees occur northward along this valley, across the highway on the Jesse Watkins farm in SW ¼, NW ¼ of the same section. Brinkman, then stationed at the Ames Forest Research Center, discovered this clone in the spring of 1949.

The largest tree of the Sherrill stand,

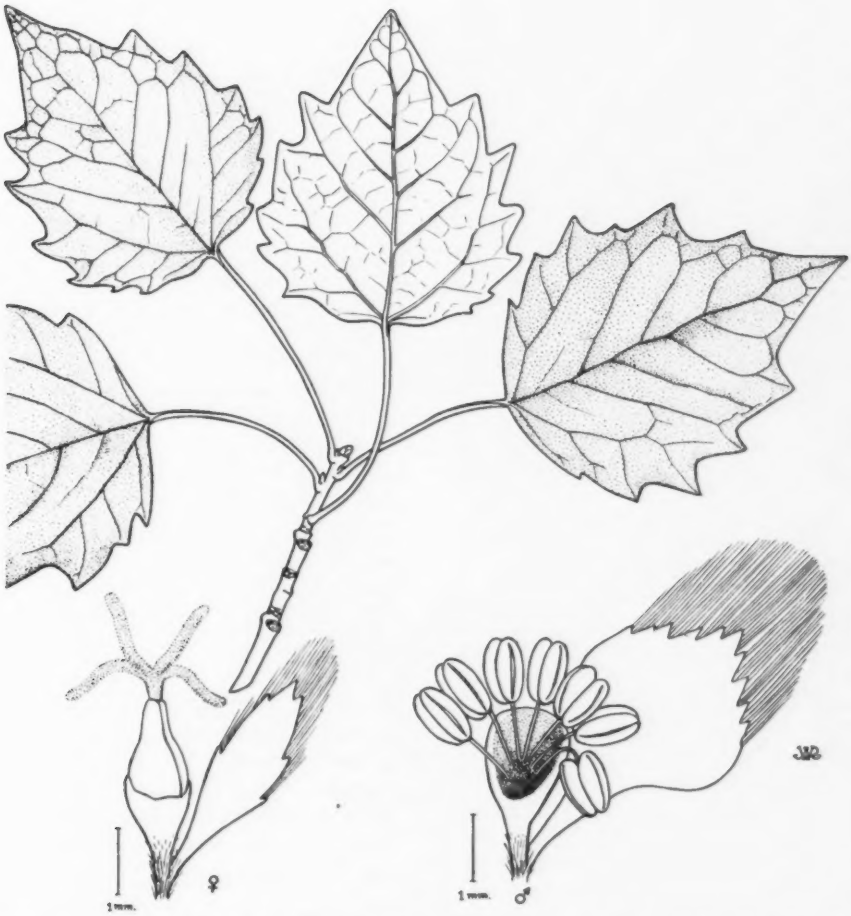

FIGURE 2. *Sherrill poplar: Leafy twig, two-thirds natural size (Brinkman, June 6, 1954); lower right, male flower with bract, × 10 (Little and Champagne 16575). Lower left, Shimek poplar: Female flower with bract, × 10 (Little and Champagne 16581). Drawn by Jane W. Roller, U. S. Forest Service.*

FIGURE 3. *Sherrill poplars on the John Sherrill farm, southeast of Keosauqua, Iowa. (U. S. Forest Service photo.)*

and apparently the original seedling, was located on the Jesse Watkins farm in a small valley a few hundred yards from the house. When cut on June 9, 1954, for studies of the wood, it was 51 years old at the stump, 70 feet high, and 24.7 inches d.b.h. Four other trees of this clone cut the same year were 36, 30, 28, and 16 years old at the stump, 53, 63, 62, and 51 feet tall, and 14.7, 11.5, 13.1, and 10.3 inches d.b.h., respectively. The largest trees in the present Sherrill stand were 30 to 35 years old and 12 to 15 inches d.b.h. in 1954 (Fig. 3). Intermittent grazing and burning of the area have resulted in an irregular stand composed of trees of various ages and sizes.

Botanical Description

Sherrill poplar is named for the late John Sherrill, the farmer who owned the land containing most of this poplar stand.

Sherrill poplar or Poplar 'Sherrill', a new natural hybrid clone (male) between white poplar and bigtooth aspen (*Populus alba* × *grandidentata*), intermediate between the parents. Rapidly growing tree in a stand larger than 2 acres, of uneven age, the largest individuals 30-35 years old, 15-19 m. (50-63 feet) high, 30-38 cm. (12-15 inches) d.b.h., the largest and apparently the original seedling 51 years old, 21 m. (70 feet) high, and 63 cm. (24.7 inches) d.b.h. when cut in 1954. Bark, twigs, winter buds, and leaves as in Shimek poplar (Fig. 2). The whitish soft wood has a wavy figure (Fig. 4).

Flowering catkins male, becoming 4-6 cm. long and 7-10 mm. in diameter, drooping, with pubescent axis, many-flowered, appearing brown because of the prominent brown bracts. At base of each flower is a hairy pedicel less than 1 mm. long and membranous light brown bract 4-5 mm. long and 2.5-3 mm. wide, broadly spatulate to ovate, the apical part irregularly dentate with short teeth less than 0.5 mm. long and fringed with conspicuous long white hairs 1.5-2 mm. long at apex. Individual flowers about 4 mm. long, the disk a funnellike cup 2-2.5 mm. long including the narrow short hairy stalk, slightly hairy at base, oblique and open on one side, margin entire, bearing 5-10 stamens, the filaments 1 mm. long and the purplish anthers 1 mm. long (Fig. 2). After discharge of pollen the catkin with bud scales is shed as a unit.

Comparison of Hybrid Clones with Parents

In many ways the hybrid clones are intermediate between the two parent species, although in others they resemble one parent more closely. Characteristics of hybrids and parents are summarized in Table 1.

Bark color is between the light gray of *P. alba* and the yellow gray of *P. grandi-*

dentata. The hybrid clones have the good form of the latter but persistent dead limbs of the former. The white tomentose surface so characteristic of the twigs, buds, petioles, and lower leaf surfaces of *P. alba* is absent except on young parts and sprout leaves.

The leaf blades, except on sprout leaves, resemble *P. grandidentata* sufficiently that they might be referred to an extreme variant of that species. A narrow-leaf variation from Quebec has been named *P. grandidentata* var. *angustata* Victorin (Montreal Univ. Lab. Bot. Contrib. 16:14, fig. 4, 1930). However, blades of the hybrid clones are noticeably narrower and longer than broad, longer pointed at apex, and with fewer marginal teeth, and not glabrous on lower surface. The petiole of the hybrid clones is flattened and turns reddish in autumn, as in *P. grandidentata.*

Female flowers of Shimek clone are intermediate. Bracts are dentate with short teeth as in *P. alba* though with few and less promnient marginal hairs, while in *P. grandidentata* the bracts have 5-7 longer lanceolate lobes. The cup-shaped basal disk is more nearly like that of *P. alba* in the margin, slightly wavy and only slightly oblique, while in *P. grandidentata* the larger, more open cup is about 2/3 the height of ovary and with crenate oblique margin. The disk is glabrous except at base in *P. alba*, slightly pubescent toward base in the hybrid, and pubescent in *P. grandidentata.*

Male flowers of Sherrill poplar, *P. alba*, and *P. grandidentata* are similar. Sherrill poplar has bracts of intermediate shape, the width broader than the elliptic bracts 2 mm. wide in *P. alba* and narrower than the broadly ovate to orbicular bracts of *P. grandidentata.* Both Sherrill poplar and *P. grandidentata* have the pedicel and base of disk slightly pubescent.

In vegetative propagation, the hybrid clones are like *P. alba* in forming root sprouts naturally and in rooting readily from twig cuttings, while *P. grandidentata* has a lower rooting capacity.

FIGURE 4. *Wavy figure in sliced veneer panel made from Sherrill poplar.* (*U. S. Forest Service photo.*)

Both hybrid clones resemble gray poplar *P.* × *canescens* (Ait.) Sm. of Europe and Asia, which is generally accepted to be of hybrid origin from *P. alba* and *P. tremula* L., European aspen. However, the leaf blade of *P.* × *canescens* differs in its elliptic to orbicular shape, acute apex, and grayish puberulent lower surface. Also, the floral bracts have 7-9 lanceolate lobes.

For forestry purposes the hybrid clones combine the desirable characters of rapid growth, good form and ease of vegetative propagation from twig cuttings or stem wood as well as from root sprouts. Shimek poplar has better form than Sherrill poplar, but the difference may be because there were so many crowded sprouts of the former after cutting of the parent tree. The

TABLE 1. Comparsion of characters of Populus alba, P. grandidentata, and the two hybrid clones.

Character	*P. alba*	Shimek poplar	Sherrill poplar	*P. grandidentata*
Bark color	Light gray	Greenish gray	Greenish gray	Yellow gray
Diamond-shaped cracks in bark	Present	Present	Present	Less pronounced
Dead limbs	Persist	Less persistent	Less persistent	Shed
Rooting from stem cutting	Readily	Readily	Readily	Less readily
Winter twigs	Whitish tomentose	Brown, glabrous or nearly so	Brown, glabrous or nearly so	Brown, glabrous or nearly so
Winter buds	Whitish tomentose	Gray puberulent	Gray puberulent	Gray puberulent to brown and nearly glabrous
Leaves:				
Petiole	Terete, white tomentose	Flattened, glabrous or nearly so	Flattened, glabrous or nearly so	Flattened, glabrous
Shape of blade	Broadly ovate	Ovate, longer than broad	Ovate, longer than broad	Broadly ovate to elliptic
Apex of blade	Acute	Acute to acuminate	Acute to acuminate	Acute
Margin	Palmately 3-5 lobed and dentate	4-8 teeth on each side	4-8 teeth on side	5-10 rounded teeth on each side
Lower surface	Whitish tomentose	Nearly glabrous except along veins	Nearly glabrous except along veins	Glabrous
Flowers:				
Sex	Mostly female (U. S.)	Female	Male	Male and female
Bract	Dentate	Dentate	Dentate	5-7 lanceolate lobes
Disk of female flowers	Margin slightly wavy and slightly oblique, glabrous except at base	Margin slightly wavy and slightly oblique, pubescent toward base		Margin crenate, oblique, pubescent

wavy figure of Sherrill poplar makes this wood desirable as a whitish veneer in wall and cabinet panels (Fig. 4). A similar figure is perpetuated by vegetative propagation in curly poplar, a clone of *P.* × *canescens*.

Specimens

Flowering specimens of the two clones as well as *P. alba* and *P. grandidentata* were collected for comparison and identification. On April 9, 1955, Little and E. Garth Champagne, then Forester in Charge,

Ames Forest Research Center, Central States Forest Experiment Station, U. S. Forest Service visited the two stands to collect specimens. Flowering was early, following unusually warm weather. On that date the male catkins of Sherrill poplar had already shed their pollen, and most of the catkins had fallen to the ground. The female catkins of Shimek poplar had begun to elongate after opening for pollination. Fruiting catkins without functional seeds were collected by McComb on April 26, 1955, when the dominant trees had already shed their catkins.

Material with female catkins of *P. grandidentata*, at the southwestern border of its range in southeastern Iowa, was obtained from a wild tree about ½ mile south of Bonaparte, less than 5 miles northwest of the stand of Shimek poplar and slightly farther from Sherrill poplar to the southwest. Female catkins of quaking aspen (*P. tremuloides*) were collected about 4 miles east of the stand of Sherrill poplar. This is the southern border of its range in eastern United States except for a few localities in northeastern Missouri. *P. alba* is not uncommon as a planted tree in Iowa.

Afterwards Little further compared the flowering specimens with material of the parent species and of gray poplar (*P.* × *canescens*) at the National Herbarium of the U. S. National Museum. C. Heimburger of the Ontario Department of Lands and Forests confirmed the identification.

Herbarium specimens of these clones from the collections cited below have been deposited in herbaria of the following institutions: U. S. National Museum, U. S. Forest Service, U. S. National Arboretum, National Museum of Canada, Iowa State College, University of Iowa, and Bailey Hortorium of Cornell University.

Shimek poplar, Poplar 'Shimek,' or Shimek clone of Iowa hybrid poplar (*Populus alba* × *grandidentata*): *Little and Champagne 16581*, April 9, 1955, twigs with female flowers, leaves from ground (holotype at U. S. National Museum); *McComb*, April 26, 1955, twigs with infertile fruits and young leaves; *Norman J. Hanson*, August 1955, twigs with foliage, sprout twigs.

Sherrill poplar, Poplar 'Sherrill,' or Sherrill clone of Iowa hybrid poplar (*Populus alba* × *grandidentata*): *Brinkman*, June 6, 1954, twigs with foliage; *Little and Champagne 16575*, April 9, 1955, twigs with old male flowers, sprout twigs, leaves from ground (holotype at U. S. National Museum); *Little and Champagne 16579*, twigs with old male flowers from the adjacent Watson farm.

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Plant Classification

By Lyman Benson. 688 pp., illus. D. C. Heath & Co., Boston. 1957. $9.00.
Review by F. H. Eyre, Society of American Foresters, Washington, D. C.

This book, written by Professor Benson, head of the Botany Department, Pomona College, is primarily an elementary text. It will be of interest to workers in forest research, who are not experts in taxonomy, as a good review reference on how plants are classified. After an introductory chapter on identification of vascular plants the book gets into the subject of classifying flowering plants. This important section is divided into four main parts dealing with vocabulary, the process of identification, preparation and preservation of plant specimens, and the basis for classification. Then follows a similar general section on gymnosperms and finally one association of species in natural vegetation. Keys carry identifications through to families only and the reader is referred to various manuals for use in determining species. The text is profusely illustrated, especially with drawings most of which were prepared by Jerome D. Laudermilk from his own dissections. Regretfully, Mr. Laudermilk did not live to see the results of his work in print. Not the least of the usefulness of this book is its glossary of some 1200 common technical terms used in plant classification.

Maturity of White Spruce Cones and Seed

BY
W. H. CRAM
H. A. WORDEN

SEED MATURITY AND VIABILITY are of paramount importance in a tree-breeding program. For this reason investigations related to seed viability have been in progress at the Forest Nursery Station, Indian Head, Saskatchewan, since 1947.

Several indices of maturity of conifer cones and seeds have been investigated. Reliable and accurate specific gravity tests for cone and seed ripeness have been reported for three pine species (Maki, 1940; Rudolf, 1940; Fowells, 1949). Specific gravity tests and cone moisture indices were reported for Colorado spruce (*Picea pungens* Engelm.) (Cram, 1956). Firmness of the cone, color and brittleness of the seed were suggested by Crossley (1953) as indices of seed maturity for white spruce (*Picea glauca* (Moench) Voss var. *albertiana* (S. Brown) Sarg.). However, these measures of maturity vary depending on the experience of the collector. The present paper reports specific gravity and moisture content investigations for determining maturity of cones of white spruce (*Picea glauca* (Moench) Voss).

Materials and Methods

In 1954 the specific gravity and moisture content of cones from seven adjacent trees of white spruce were investigated. Cones from all trees were harvested on September 6 and natural seed shed of one tree (54-7) began on September 7. Specific gravity of a "bulk" sample of 25 cones was calculated from the loss in weight of the sample in distilled water. Moisture content of a sample of five cones was determined from the loss in weight when oven-dried at 100°C for 24 hours.

Two 40-year-old trees of white spruce with large crops of cones were selected for a more extensive study in 1955. Both trees had a southern exposure in a plantation on the Forest Nursery Station. Cones were collected at four weekly intervals from August 3 to August 24, 1955. Natural seed shed, which was hastened by hot weather, began on August 28 for tree W-2 and on August 30 for tree W-1. Each collection consisted of 150 cones, which were harvested from comparable branches on the two trees. All cones with visual insect or other damage were discarded. One sample of 50 cones and three samples of five cones were drawn at random from the remainder for each tree. Specific gravity and moisture content determinations were made immediately. Specific gravity was calculated from the loss in weight in distilled water, first, for the three "bulked" samples of five cones each, then for each individual cone in the 50-cone samples. Moisture content on a fresh weight basis was calculated from the loss in weight of

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Contribution No. 896 from the Horticultural Division, Experimental Farms Service, Department of Agriculture, Ottawa, Canada. The authors are Plant Breeder and Plotman, respectively, Forest Nursery Station, Indian Head, Saskatchewan, Canada.

the same three bulked samples after drying in an oven for 48 hours at 100°C. The 50 cones were then segregated into their respective gravity classes, and allowed to dry under solar heat in a greenhouse. Seed was extracted from the cones in each specific gravity class on September 23 by shaking in a screen box to simulate commercial methods. The winged seed were gently rubbed and cleaned with a South Dakota Seed Blower. The sound seed were weighed and counted. Both the weight per thousand seeds and seeds per cone were calculated.

Viability of the 1955 seed from the various dates of harvest for both trees was determined in a greenhouse germination test in 1956. Findings from a previous study on the control of damping-off diseases (Cram and Vaartaja, 1957) were applied with excellent results. The sowing plan was a randomized block with four replications and 100 seeds per plot. A record was made of emergence (i.e. apparent germination) every second day from March 19 to April 6. Data for the apparent germination in 21 days were transformed and subjected to analysis of variance to determine the significance of mean differences. The non-germinated seed were then removed and classified as sound, rotten, or empty (abortive).

In 1956 the white spruce seedcrop was exceptionally light and was further reduced by a severe infestation of the spruce seedworm (*Laspeyresia youngana*). As a result, attempts to duplicate the large sample study of 1955 were restricted in 1956 to a different and single tree (42-2). Two hundred cones were collected on three dates, namely, August 2, August 16 and August 23. Samples of 100 cones were drawn from these collections and the specific gravity determined for each individual cone. Subsequent treatment of the 1956 cones and seed was identical to that outlined above for the 1955 cones. An attempt was also made in 1956 to duplicate the small sample technique employed in 1955. Six apparently sound cones were harvested at random from two mature trees at five weekly intervals. Specific gravity determinations were made for each cone. Moisture content was determined for the same six cones but as two samples of three cones each. Seedworm damage apparently caused some cones to open prematurely on August 27 for one tree (54-2), and on August 31 for the other tree (42-2).

Results

The respective specific gravity and moisture content values for cones of seven trees of white spruce on September 6, 1954, are listed in Table 1. There was a close relationship between the two proposed indices of cone maturity as indicated by a correlation value of 0.98. It would appear that trees within the species differed with respect to maturity of cones on September 6. Natural shedding of seed (hereafter termed seed-shed) occurred when either the specific gravity of the cones reached 0.48, or moisture content was 28 percent.

A gradual decrease in the specific gravity of the cones during the five weeks preced-

TABLE 1. Specific gravity and percent moisture content of cones collected from seven trees of white spruce on September 6, 1954.

Tree	Specific Gravity[1]	Moisture Content[2] percent
54-7[3]	0.4867	28.2
54-3	0.5300	32.1
54-6	0.5889	36.4
54-4	0.6227	38.7
54-2	0.7109	45.6
42-2	0.8352	49.2
54-5	0.9115	57.7

[1]Specific gravity for a bulk sample of 25 cones.
[2]Moisture content (%) for a sample of 5 cones.
[3]Natural seed-shed for 54-7 occurred on September 7.

ing natural seed-shed was apparent from the 1955 data listed in Table 2. Ninety-two percent of the cones of one tree (W-2) had a specific gravity below 0.804 four days prior to natural seed-shed, and 92 percent of the cones of the other tree (W-1) had a specific gravity below 0.864 six days prior to natural seed-shed.

Specific gravity of cones gradually decreased with each subsequent harvest in 1956 (Table 3) as in 1955. However, a marked similarity was revealed for the specific gravity distribution and mean for August 23, 1956, (Table 3) and for August 17, 1955, (Table 2). This was interpreted as proof that maturity of white spruce cones occurred somewhat later in 1956 that in 1955. Observations on natural seed-shed in 1955 and 1956 supported this evidence.

The gradual decrease in specific gravity and moisture content of the cones with approaching natural seed-shed in 1955 should be noted in Table 4. At the same time, there was an increase in the amount of sound seed extracted from the cones. On the other hand, viability of the seed

TABLE 2. Frequency distribution of specific gravity for 50 cones from each of two white spruce trees at four weekly intervals in 1955.

Specific gravity class	Date of harvest Aug. 3	Aug. 10	Aug. 17	Aug. 24
	Percentage of cones in each harvest			
0.714-0.743	....	....	....	19
0.744-0.773	....	....	....	38
0.774-0.803	....	....	....	32
0.804-0.833	....	....	....	6
0.834-0.863	....	....	....	1
0.864-0.893	....	....	....	2
0.894-0.923	....	....	2	2
0.924-0.953	....	....	20	....
0.954-0.983	....	....	43	....
0.984-1.013	2	26	33	....
1.014-1.043	54	65	2	....
1.044-1.073	44	9	....	....
Mean S. G.	1.04	1.02	0.97	0.78

TABLE 3. Specific gravity distribution by classes for cones from one white spruce tree [42-2], at three dates of harvest in August 1956, with characteristics of the respective seed.

Specific gravity classes	Cone Distribution[1] Aug. 2	Aug. 16	Aug. 23	Seeds per cone[2] Aug. 2	Aug. 16	Aug. 23	Seed weight[3] Aug. 2	Aug. 16	Aug. 23
	percent			*number*			*grams*		
0.868-0.897	....	....	6	....	....	38	....	....	3.1
0.898-0.927	....	....	5	....	....	28	....	....	3.1
0.928-0.957	....	....	25	....	....	34	....	....	3.1
0.958-0.987	1	....	37	12	....	39	1.9	....	2.9
0.988-1.017	2	3	23	21	17	40	2.2	3.0	2.9
1.018-1.047	18	32	4	26	39	41	2.6	3.0	2.5
1.048-1.077	69	65	....	47	55	....	2.8	3.1	....
1.078-1.107	10	....	....	62	....	....	2.9	....	....
Mean values	1.048	1.050	0.967	44	49	38	2.5	3.0	2.9

[1]Percentage of cones in each specific gravity class.
[2]Sound seeds per cone in same for respective cones.
[3]Air dried weight in grams per 1000 seeds in November 1956.

TABLE 4. Characteristics of cones and seed from two white spruce trees at four weekly intervals in 1955.

Tree	Date of harvest	S. G. of cones[1] single	S. G. of cones[1] bulk	Cone[2] moist.	Seeds[3] cone	Germ.[4]
W-1	Aug. 3	1.041	1.044	60.2	32.0	86.7[6]
	Aug. 10	1.032	1.052	60.7	36.3	78.4
	Aug. 17	0.986	1.028[5]	59.5	37.6	78.8
	Aug. 24	0.775	0.800[5]	49.8[5]	58.8	81.5
W-2	Aug. 10	1.015	1.012	59.0	26.0	49.8
	Aug. 17	0.961	0.963[5]	59.3	20.2	52.3
	Aug. 24	0.767	0.744[5]	48.2[5]	27.1	77.5[6]

[1]Mean specific gravity for 50 individual cones and for 3 samples of 5 "bulked" cones.
[2]Mean moisture content for same 3 samples of 5 cones.
[3]Mean number of sound seed extracted per cone.
[4]Mean germination or emergence as percentage of stratified seed sown.
[5]Significantly less than for preceding date of harvest.
[6]Significantly greater than for other dates of harvest of same tree.

appeared to decreased or increase with maturity depending on the seed tree.

Both indices of cone maturity given in Table 4 demonstrated that cones of tree W-2 were riper on August 24 than those of tree W-1. Specific gravity was clearly the more precise index, in that it demonstrated the ripening process was in progress two weeks prior to natural seed-shed. Moisture content proved less accurate, in that it showed no indication of approaching cone maturity until four to seven days prior to seed-shed. Nevertheless, the respective values for the two indices in 1955 were positively related, as indicated by a correlation value of 0.98. An identical relationship was apparent between the specific gravity values in Table 4 which were derived from individual cones and from small bulk samples of cones.

Seed weight data for the various dates of harvest in 1956 would suggest a trend towards increased weight as the cones ripened. Average weight of the seed apparently increased from 2.5 to 3.0 grams per 1000 in the period August 2 to August 16 (Table 3). Little to no change in weight of seed was manifested a week later, some eight days prior to seed-shed. The low weight of seeds from the cones which fell into the higher specific gravity classes on August 23 was most likely due to damage by the spruce seedworm. Nevertheless, it would appear that development of white spruce seed continues to within two weeks of natural seed-shed.

Germination of white spruce seed would appear to be dependent on the inherent characteristics of the parental seed tree as well as the stage of development at harvest. Seed harvested from one tree (W-2), on August 24 exhibited 50 percent greater germination than that harvested one or two weeks earlier in 1955 (Table 4). On the other hand, seed harvested from another tree (W-1) on August 3, 1955, demonstrated five to eight percent more germination than that harvested during the three following weeks. The post-germination seed-cutting test revealed that some seed, which was harvested from both trees on August 10 and 17 had decayed. The percentage of decayed seed decreased as the season progressed from 12 to 8 percent for tree W-1, and from 34 to 13 percent for tree W-2 during the period August 10 to August 24. The percentage of sound non-germinated seed was almost identical

for all dates of harvest, and averaged six percent for tree W-1 and 10 percent for tree W-2. Only one percent of the non-germinated seed proved to be empty. The non-germinated seed, which proved to be decayed or rotten, may have been injured during the seed cleaning process. From 10 to 25 percent of the seed required excessive rubbing to completely remove the wings. It is suggested that these seeds were abortive or under-developed and were frequently damaged. As a result, apparent germination data demonstrated that maximum viability of white spruce seed is attained four weeks prior to natural seed-shed for one tree, and one week prior to seed-shed for the other tree.

Maximum production of white spruce seedlings resulted only when the cones were harvested approximately one week prior to natural seed-shed. From an economic viewpoint, it is desirable to achieve maximum production of seedlings per cone harvested. From the seed-per-cone and germination data listed in Table 4, it was evident that production per cone was materially increased only on the last harvest date. In other words, by delaying the harvest of cones until just one week prior to natural seed-shed it was possible to increase seedling production by 50 percent over all previous harvests.

The 1956 data for specific gravity and moisture content of cones which have been harvested from two trees at four weekly intervals in 1956 have been summarized in Table 5. Data for both indices revealed the ripening process of the cones despite damage by insects. It would appear that white spruce cones should be harvested somewhat earlier in years or in areas in which infestations of the spruce seedworm are severe.

Discussion and Conclusions

Maximum yield of seedlings per cone is essential to a tree breeding program, as well as being of economic importance to seed collectors and nurserymen. In this study, yield and viability of white spruce seed were found to be directly influenced by the maturity of the cones at harvest. Size of seed as manifested by weight appeared to increase until two weeks prior to natural seed-shed (Table 3). Yield of seed increased 40 percent and germination 14 percent in the three-week period just prior to seed dispersal. As a result, seedling production reached a maximum when harvesting of cones was delayed until three to six days before natural seed-shed.

Specific gravity and moisture content determinations proved reliable indices for maturity of cones and of seed from white

TABLE 5. Specific gravity and moisture content of cones from two white spruce trees at five weekly intervals in 1956.

Date of Harvest	Specific Gravity[1]			Moisture Content[2]		
	42-2	54-2	Mean	42-2	54-2	Mean
July 31	1.022	1.043	1.032	62.4	62.7	62.6
Aug. 7	1.055	1.045	1.050	58.6	60.8	60.0
Aug. 14	1.051	1.033	1.042	58.1	61.6	59.8
Aug. 21	1.019[3]	0.904[3]	0.961	55.5[3]	57.8[3]	56.6
Aug. 28	0.827[3]	.....[4]	.....	53.4[3]	.....[4]	.....

[1]Average specific gravity of six individual cones.
[2]Percentage moisture content for two samples of three cones.
[3]Significantly less than value for preceding date.
[4]Shedding seed prematurely due to severe insect infestation; 42-2 started to shed seed on August 31.

spruce. The two indices were closely associated in a positive manner for three consecutive years. Both the specific gravity and moisture content of white spruce cones manifested a gradual decrease in the weeks preceding natural seed dispersal (Tables 1, 4, 5). In addition, maturity of the cones at harvest had a direct influence on the yield and viability of the seed extracted from them (Table 4).

Differences with respect to maturity of the cones were found to exist between cones on the same tree, between years for the same tree, and between trees in the same year. Specific gravity of cones, which were harvested from tree W-1 on August 24, 1955, varied from 0.715 to 0.904 (Table 2). Cones from tree 42-2 had an average specific gravity of 0.835 on September 6, 1954 (Table 1), and a specific gravity of 0.827 on August 28, 1956 (Table 5). In all three years marked differences in specific gravity of cones were noted between individual trees under investigation (Tables 1, 4 and 5).

To sample the maturity of white spruce cones the technique must resolve variations between cones. Six to ten random cones should give a reliable picture of maturity because of the close relationship found between maturity indices for small and large samples (Table 4). Moisture content tests for three lots of two cones each, or specific gravity determinations of six individual cones, will provide an accurate measure of seed ripeness. Harvesting of cones which are produced in a breeding program should commence once average moisture content falls to 48 percent or specific gravity of the open-pollination cones falls to 0.744. Before harvesting a white spruce tree, commercial seed collectors are advised to test 10 fresh cones in a jar of turpentine or kerosene. Maximum yield and weight of seed will be obtained if collection is delayed until nine of the 10 cones float in turpentine, or eight of the 10 cones float in kerosene.

Variations in the date of natural seed-shed would appear to be directly related to similar differences in dates of shedding of the pollen for white spruce. Phenological data, which have been collected at the Forest Nursery Station since 1947, demonstrated that natural seed-shed occurred from 97 to 99 days after shedding of the pollen. The date of pollen shedding in 1948, 1954, 1955 and 1956 varied from May 21 to May 31, while that of natural seed-shed ranged from August 28 to September 7. Seed-shed was reported (Crossley, 1953) to begin on September 19 at Kananaskis in 1952. This would be approximately 108 days after pollen started to shed at Indian Head, namely on June 3, 1952. It is possible that pollen-shed was some nine days later at Kananaskis than at Indian Head due to an increase of 1364 feet in altitude. Therefore, one should be prepared to test the maturity of white spruce cones approximately 90 days after pollen-shed occurs in the area.

Summary

Specific gravity and moisture content proved reliable and accurate indices of cone and seed maturity for white spruce (*Picea glauca* (Moench) Voss). Large and small samples of cones were harvested from two or more trees for determinations in 1954, 1955 and 1956. A positive correlation (0.98) was found to exist between the respective values for specific gravity and moisture content of the cones in all years. Specific gravity of individual white spruce cones varied from 1.06 to 0.71, and on the average, decreased from 1.04 to 0.77 in the four weeks just prior to natural seed-shed. On the average, the respective moisture content decreased from 60.7 percent to 48.2 percent. Differences with respect to maturity of the cones were found to exist between cones on the same tree, between years for the same tree, and between trees in the same year.

Date of seed-shed in white spruce was

found to be directly related to the date of pollen-shed for four years in which data were available. On the average, natural seed dispersal occurred 98 days after pollen-shed. It is suggested that cone maturity tests for white spruce should be made 90 days after pollen-shed.

It is recommended that maturity tests be conducted on six to 10 fresh cones harvested at random from each tree. Average moisture content for three samples of two cones each, or average specific gravity of six individual cones will provide an accurate measure of seed ripeness. Cones should be collected when the moisture content (wet weight) falls to 48 percent, or specific gravity reaches 0.74. Commercial seed collectors should test 10 fresh cones in a jar of turpentine or kerosene, and collections should be delayed until nine cones float in turpentine or eight in kerosene.

Size of seed appeared to increase with cone maturity within two weeks of natural shed. Yield of seed increased 40 percent and germination of stratified seed increased 14 percent in the last four weeks of maturity. Maximum yield of seedlings per cone was obtained when harvesting was delayed until 3 to 6 days before natural seed dispersal.

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Estimation of Forest Management Inventory Data from Aerial Photographic Measurements

BY
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WITHIN RECENT YEARS attempts have been made to utilize vertical aerial photographs in almost every phase of forest management work. Most of this activity has been in the nature of timber stand inventory, and the extent of aerial photographic application has varied considerably. In some instances the aerial photographs have served only as a guide for the movement of field crews, whereas in others they have been used directly for volume determination.

Investigations of the use of aerial photographs in inventory procedure have been numerous, but have been largely confined to the determination of existing timber volume with but little thought given to the determination of more detailed and qualitative type information. However, some work has been conducted for the specific purpose of investigating the possibility of determining this type of information from aerial photographs. This work is covered in articles or comments on: growth (Spurr, 1948), age (Krutzsch, 1925; Jacobs, 1932; Andrews, 1934; Stevens, 1949; Spurr, 1953), stem diameter (Zieger, 1928; Spurr, 1948 and 1952; Nash, 1948; Minor, 1951; Ferree, 1953), stem form (Grumbine, 1948; Spurr, 1948), stem quality (Grumbine, 1948; Spurr, 1948), and reproduction (Mignery, 1951; Ker, 1953). The reports or comments by the above mentioned individuals are in some cases inclusive of several species and a single variable or a limited number of variables for several species, but in none of these cases has a study been made of the determination of all possible variables for a given species.

The primary purpose of this study was to investigate the possibility of determining a maximum amount of detail and qualitative information for the longleaf-pine type (*Pinus palustris* Mill.) from aerial photographs. This was to be accomplished by determining those relationships between this qualitative information and the stand information that can be measured or recognized directly on aerial photographs. The qualitative information could thus be determined indirectly from the measurable factors.

This was not a study of cause-effect relationships but rather a study to determine the trends of existing relationships and their extent. Neither was the purpose of the study to determine relationships that may exist in the longleaf-pine type in other areas or in other types but only to determine the relationships that may exist for a specified type.

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Study Methods

Sample plots. Sixty-five square sample plots one-tenth acre in size were located in 13 stands of second growth longleaf-pine type. The area selected for the study was in northeast Florida and had not been disturbed by harvest cutting or fire for approximately 15 years. The stands were selected by photographic interpretation on the basis of: (1) uniformity within each stand in regard to tree size and area distribution, and (2) a distribution, between plots, of the various stand conditions that existed for longleaf pine within the study area.

Information collected. On each plot, measurements were made of all tree and stand variables. These included factors which could be measured either directly on aerial photographs or only on the ground.

In order to keep the field work within reasonable limits, a stratified subsample of six trees was selected on each plot. The stratification was on a basis of diameter at breast height (d.b.h.). The following factors were measured for each tree:

1. Tree height
2. Crown diameter
3. Percentage of tree height in crown
4. Age at breast height
5. Radial growth at breast height
6. D.B.H.

The remaining information was collected on a plot basis as follows:

1. Ground cover
2. Drainage conditions
3. Silvicultural conditions
4. Number of trees per d.b.h. class
5. Amount of reproduction

In the office, arithmetic averages were computed from the six sample trees for height, age, radial growth, crown diameter, d.b.h. and percentage of tree height in crown for each plot. The crown density and cubic volume were then determined for each plot.

Preliminary analysis. Three stand variables were discarded either during the collection of the field data or before the preliminary analysis was made. These stand variables were *ground cover, drainage conditions* and *silvicultural conditions.* Ground cover was discarded as 35 of the original 65 sample plots were in a single ground-cover classification. Silvicultural conditions and drainage conditions were not considered further since their descriptions were too subjective in nature to be classified consistently.

A graph was then drawn from each possible pair of the 10 remaining variables, regression coefficients were computed and the corresponding correlation coefficients were determined. The correlation coefficients are listed in Table 1. Two additional variables were eliminated at this point. The *amount of reproduction* was eliminated as it was not found to be sufficiently related to any other variable to be of any future use. Although the *percent of tree height in crown* exhibited definite relationships to several other variables, it could add very little to this study since it could not be measured directly on photographs with any accuracy and had but little value as an indirect measurement.

Final analysis. The elimination of these variables left eight stand variables for further analysis. The eight variables could logically be separated into two groups: independent variables and dependent variables. The independent variables were those that could be measured directly on aerial photographs and included *height, crown diameter, crown density* and *number of trees per acre.* The dependent variables were those that could not be measured directly on aerial photographs but which exhibited correlation with one or more of the independent variables. This group of variables was composed of *radial growth, d.b.h., age* and *cubic volume.*

The correlation coefficients indicated that no indirect measurement could be determined with precision from a single direct measurement; therefore, a multiple regression analysis was made to determine the possible linear or curvilinear relation-

TABLE 1. Correlation coefficients[1] for each paired combination of stand variables in the longleaf-pine type (Pinus palustris *Mill.*) *based on 65, one-tenth acre sample plots.*

	Tree Height (feet)	Crown Diameter (feet)	Crown Density (percent)	Number of Trees	Radial Growth (inches)	Age (years)	D.B.H. (inches)	Volume (cu. ft.)	Percent in Crown	Amount of Reproduction
Tree Height (feet)	—	.201	.415	.302	—.587	.784	.513	.640	—.455	—.194
Crown Diameter (feet)	.201	—	.248	—.417	—.112	.332	.822	.004	.293	—.208
Crown Density (Percent)	.415	.248	—	.720	—.546	.526	.172	.780	—.467	.050
Number of Trees	.302	—.417	.720	—	—.473	.328	—.358	.749	—.672	.266
Radial Growth (inches)	—.587	—.112	—.546	—.473	—	—.836	—.238	—.625	.655	.148
Age (years)	.784	.332	.526	.328	—.836	—	.540	.683	—.556	—.254
D.B.H. (inches)	.513	.822	.172	—.358	—.238	.540	—	.210	.127	—.249
Volume (cu. ft.)	.640	.004	.780	.749	—.625	.683	.210	—	—.637	—.005
Percent in Crown	—.455	.293	—.467	—.672	.655	—.556	.127	—.637	—	—.062
Amount of Reproduction	—.194	—.208	.050	.266	.148	—.254	—.249	—.005	—.062	—

[1]A correlation coefficient, for 65 plots, of 0.316 is significant at the one percent level, and 0.243 is significant at the five percent level.

ships that existed between combination of variables. The relationships were determined by using the four independent measurements with each of the dependent measurements separately. These were tested by the variance-ratio technique (Fisher's "F" test). All significant relationships were found to be linear. In no case did the curvilinear relationships give results that were significantly different from those found in the analysis of linear relationships. Beyond the limits of the sample, however, the relationships may be curvilinear as this biological phenomenon was indicated when only two variables were compared.

Results

Using the independent values that were significantly related to the dependent values, formulae were derived for estimating values of each dependent variable. The results of the analysis for linear relationships and the derived formula are presented for each dependent variable in the following sections.

Radial growth at D.B.H. Radial growth at d.b.h. was found to be significantly related to height and crown density at d.b.h. at the one percent level.

The formula for linear estimate of radial growth is:

$$Y_1 = 1.07 - 0.0111X_1 - 0.00381X_3$$

Where:

Y_1 = radial growth in inches at d.b.h. during the last five years.
X_1 = tree height in feet.
X_3 = crown density in percent.

Age at D.B.H. Age at d.b.h. was found to be significantly related to height and crown density at the one percent level.

The formula for the linear estimate of radial growth is:

$$Y_2 = -15.0 + 0.78X_1 + 0.11X_3$$

Where:

Y_2 = age at d.b.h.
X_1 = tree height in feet.
X_3 = crown density in percent.

D.B.H. D.b.h. was found to be significantly related to crown diameter, height and number of trees at the one percent level.

The formula for the estimate of d.b.h. is:

$$Y_3 = 0.6 + 0.2981X_2 + 0.0843X_1 - 0.0331X_4$$

Where:

Y_3 = d.b.h. in inches.
X_2 = crown diameter in feet.
X_1 = tree height in feet.
X_4 = number of trees per one-tenth acre.

Merchantable cubic volume. Merchantable cubic volume was found to be significantly related to height, crown density and number of trees at the one percent level.

The formula for the estimate of merchantable cubic volume is:

$$Y_4 = -114.0 + 1.111X_3 + 3.030X_1 + 2.375X_4$$

Where:

Y_4 = merchantable cubic volume inside bark for trees four inches d.b.h. and over to a four inch top (inside bark) per one-tenth acre.
X_3 = crown density in percent.
X_1 = tree height in feet.
X_4 = number of trees per one-tenth acre.

Discussion

Errors in the determination of radial growth, age, d.b.h. and cubic volume from these related directly-measurable factors stem from two sources: (1) the inaccuracy in making the direct measurement and (2) the unaccounted-for variance attributable to stand and tree factors that have not been considered.

In the use of these direct measurements, it must be assumed that the accuracy obtainable in the measurement of these significantly related variables is:

Height: 10-foot classes
Crown Density: 10 percent classes
Crown Diameter: 3-foot classes
Number of Trees: within 20 percent of actual.

This accuracy is possible when the measurements are made by competent photo interpreters on good quality photographs at a scale of 1:15840 or larger.

In addition, it must be assumed that the variance in radial growth, age, d.b.h. and volume, which is not accounted for by these significantly related variables, is without bias. If these assumptions can be made, and the accuracy described above is possible, then, 95 times out of 100, the sampling precision obtainable in the estimation of radial growth, age, d.b.h. and volume of a homogeneous stand or type is:

Radial Growth: ± .044 inches of actual average growth rate with 44 photographic sample plots.
Age: ± 2.5 years of actual average age with 12 photographic plots.
D.B.H.: ± .74 inches of actual average d.b.h. with two photographic plots or ± .37 inches of actual average d.b.h. with seven photographic plots.
Volume: ± 9.6 cubic feet of actual volume with 29 photographic plots.

The number of plots required in each of the above cases is sufficient to produce the accuracy shown only when the means of the sample plots are within the limits of the original data and at or near the means of the original data used in this study. If the means of the sample data are not within these limits, then no statement of accuracy can be made.

The limits of the original data are:
Average Tree Height: 34 to 60 feet.
Crown Density: 6 to 72 percent.
Average Crown Diameter: 7 to 20 feet.
Number of trees: 4 to 42 per one-tenth acre.

The above stated relationships and expected accuracy in the determination of indirect measurements apply only to the longleaf-pine type as found in the study area. Since only 13 forest stands were used in the determination of these relationships, care must be exercised in the projection of these relationships to longleaf-pine stand conditions not present in the sample,

or to other forest types. While the relationship found to exist in this study would not be expected to apply directly to other species in this or other areas, similar relationships may be found to exist.

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Importance of Mycorrhizae to Ponderosa Pine Seedlings

BY
ERNEST WRIGHT

GOOD DEVELOPMENT of ectotrophic mycorrhizae on the roots of forest tree seedlings is generally accepted as necessary for good survival and good growth. This is especially true in afforestation (Kessel, 1927; Hatch, 1937; Rosendahl and Wilde, 1942). Results of recent tests in the Pacific Northwest emphasize the importance of mycorrhizae in seedling survival and development.

Mycorrhizae on higher order plants have long been investigated by foresters and botanists. Comprehensive reviews of the literature have been made by Rayner (1927), McArdle (1932), Hatch (1937), Bjorkman (1949), and Kelley (1950). Mycorrhizae on ponderosa pine were observed by McComb (1943) on seedlings in a forest nursery at Ames, Iowa, but his critical studies were mostly on other tree species. Stoeckeler[1] studied mycorrhizae of ponderosa pine (*Pinus ponderosa* Laws.), jack pine (*Pinus banksiana* Lamb.), and blue spruce (*Picea pungens* Engelm.) at Forest Service nurseries in North Dakota in the late 1930's. Thomas (1943) recorded the presence of coralloid mycorrhizae on ponderosa pine in Colorado.

At the Towner, N. Dak., nursery, Stoeckeler found ponderosa pine to be less responsive to mycorrhizae than either jack pine or blue spruce. However, in a tree nursery at Oakes, N. Dak., he found the reverse was true. Here the soil was alkaline, and phosphate starvation was often striking in nonacidified seedbeds. A combination of acidification and inoculation, using moist mycorrhizal soil, resulted in a noticeable increase in the percentage of plantable 2-0 ponderosa pine stock.

All these studies were made with the Rocky Mountain form of ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.). This paper reports tests with ectotrophic mycorrhizae on ponderosa pine in the Pacific Northwest.

The Problem

Development of fungal symbionts on nursery stock is encouraged by soil acidification (Young, 1938) and the application of fertilizers (McComb, 1943). On the

[1]Stoeckeler, J. H. Memorandum designated RS-LS-Regeneration, Nursery, Fn-2. U. S. Forest Service, Feb. 10, 1940. Also, memorandum dated October 19, 1955.

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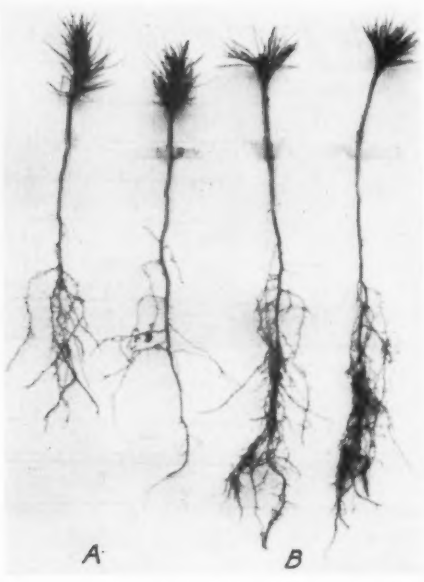

FIGURE 1. *One-year-old ponderosa pine seedlings. A. From untreated (not fumigated) soil. Shows start of mycorrhizal formation on roots. B. From fumigated soil. Seedlings lack mycorrhizae but have a better developed root system.*

other hand, weed eradicants, soil sterilants, and toxic chemicals retard their development (Wilde, 1954).

In 1950, fumigants—such as chloropicrin, methyl bromide and ethylene dibromide—were first used to control a *Fusarium* root rot in ponderosa pine seedbeds of a Pacific Northwest forest nursery. Soil was fine sandy loam (pH 6.5). In the first growing season, seedlings in the chloropicrin-fumigated beds appeared greener and more thrifty than those in untreated soil (Fig. 1). By the second year, however, seedlings in the fumigated beds were stunted and chlorotic (Fig. 2 and Table 1). Examination of the roots revealed that they uniformly lacked mycorrhizae, while roots of normal seedlings in untreated soil showed an abundance of mycorrhizae. These mycorrhizae were white to grey in color, were formed typically as ectotrophic mantles over the root tips, and were commonly dichotomously branched.

A number of tests were made to compare the response of mycorrhizal and nonmycorrhizal seedlings to field planting. If survival and development of these nonmycorrhizal seedlings followed the same pattern as that established previously, fumigation to solve one problem was merely creating another.

Field Test Plantings

Three preliminary test plantings were made with 800 seedlings in April 1951. The largest 2-0 nonmycorrhizal ponderosa pine seedlings available were sorted from stock grown in fumigated soil. Normal-sized mycorrhizal seedlings, of the same age but somewhat larger, were obtained from stock

TABLE 1. Average development of ponderosa pine seedlings on fumigated (1950) and untreated soil.

Stock and soil treatment	Tops			Roots			Mycorrhizae
	Length	Spread	Dry weight	Length	Spread	Dry weight	
	Inches	*Inches*	*Grams*	*Inches*	*Inches*	*Grams*	
1-0 stock (Av. 50 seedlings):							
Fumigated	2.73	1.00	0.240	7.73	3.50	0.250	None
Untreated	2.75	1.25	0.210	8.08	3.37	0.136	Few
2-0 stock (Av. 50 seedlings):							
Fumigated	3.88	1.84	0.352	9.33	8.95	0.300	Trace
Untreated	4.71	5.38	1.814	9.24	10.30	0.994	Abundant

already sorted for field planting. Then, both mycorrhizal and nonmycorrhizal seedlings were hand planted in alternate rows by regular Forest Service crews. The test plots were established on burned-over lands in the Tumalo, Two Springs, and Lava Butte areas of the Deschutes National Forest.

The mycorrhizal stock showed a higher percentage of survival than the nonmycorrhizal seedlings at the end of the first growing season (Table 2). Statistical tests indicate that the better survival of stock with mycorrhizae was not an accident of sampling. However, difference in size may have influenced survival.

Deer damage was very heavy on the Tumalo and Two Springs plots in the late fall and following spring. Therefore, no reliable data on survival could be obtained after 1 year. Re-examination of seedlings in the Lava Butte plot, however, showed that the stock originally nonmycorrhizal was dying at a decreasing rate each year. Random samples showed that mycorrhizae had been acquired either from adjacent mycorrhizal stock or from mycorrhizal fungi in the soil. The difference in size continued for 3 years, becoming less each year.

The following year 2-0 ponderosa pine seedlings from fumigated beds were carefully sorted and those showing mycorrhizae were discarded. Seedlings of the same size and age with abundant mycorrhizae were obtained by sorting stock grown in untreated soil. A thousand seedlings were machine planted at each of two test locations on the Deschutes National Forest in central Oregon, by Forest Service planting crews in mid-April 1952. Five rows of 100 seedlings with mycorrhizae were alternated with an equal number of seedlings without mycorrhizae at each location. Survival counts were made at several intervals after planting and at the end of the first growing season.

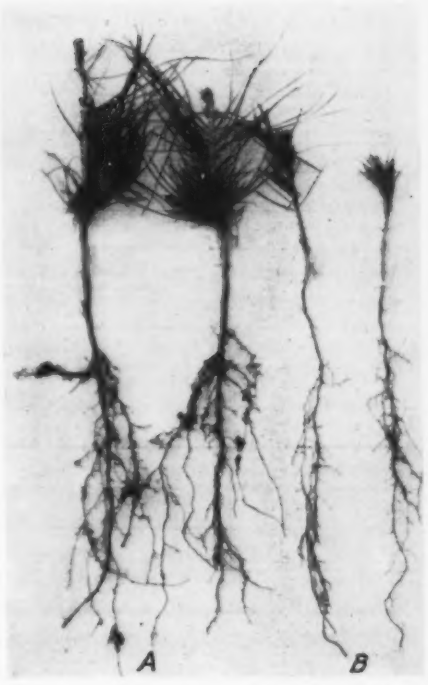

FIGURE 2. *Two-year-old (2-0) ponderosa pine seedlings. A. From untreated (not fumigated) soil. Roots show numerous mycorrhizae and seedlings are now normal size for 2-0 stock. B. From fumigated soil. Seedlings lack mycorrhizae and are no larger than 1-0 stock.*

The South Lava Butte plantation, on an excellent pine site, showed significantly better survival throughout the first growing season for the stock with mycorrhizae (Table 3). However, the poor East Lava Butte location failed to show significantly better survival for mycorrhizal stock at any time after planting. The very unfavorable growing conditions there, probably due to the heavy growth of bunchgrass, apparently were sufficient to counteract the benefit of mycorrhizae. Both plantings constituted severe tests, because 1952 was abnormally dry prior to and during the growing sea-

TABLE 2. Field survival of nonmycorrhizal and mycorrhizal 2-0 ponderosa pine 6 months after planting, 1951, Deschutes National Forest, Oregon.

Field planting plots (formerly forested)	Stock without mycorrhizae[1]		Stock with mycorrhizae[2]	
	Planted	Living	Planted	Living
	Number	*Percent*	*Number*	*Percent*
Tumalo (poor site, recent burn; fine sandy pumice)	100	59	100	75
Two Springs (fair site, recent burn, heavy brush; rocky, sandy loam)	50	40	50	92
Lava Butte (Excellent site, old burn; coarse sandy pumice)	250	83	250	96
Average		60.7		87.7

[1]From gas-fumigated soil, stunted and chlorotic.
[2]From soil not fumigated, normal-sized.

son. However, the stock was of equal size, although somewhat smaller than normal, and a direct comparison of survival is believed justified.

At the time the test plantations were established, larger 2-0 mycorrhizal stock was machine planted in adjacent areas by regular Forest Service crews. Survival at the end of the 1952 growing season for normal-sized seedlings in the South Lava Butte area was 99 percent, while in the East Lava Butte, it was 92 percent. Planting loss in the South and East Lava Butte test plots for the undersized stock was appreciable (Table 3). A check of mycorrhizal seedlings in both test plots after 6 weeks showed 6 percent of the loss was due to faulty planting (mostly too deep). There was also some loss due to shallow planting, which permitted the roots to dry out.

TABLE 3. Survival of equal-sized but smaller than normal nonmycorrhizal and mycorrhizal 2-0 ponderosa pine, 1952, Deschutes National Forest, Oregon.

Plot	Mortality[1]				Diff. required for significance at 5% level
	Examined after—	Without mycorrhizae	With mycorrhizae	Difference	
		Percent			
South Lava Butte (good site; formerly forested)	6 wks.	18.2	7.0	11.2	5.12
	2½ mo.	31.0	17.4	13.6	7.23
	5 mo.	64.2	47.2	17.0	16.04
East Lava Butte (poor site; bunchgrass, Idaho fescue)	6 wks.	31.2	23.8	7.4	13.91
	5 mo.	70.8	68.2	2.6	12.60

[1]Based on 1,000 machine-planted seedlings in rows of 100 each at each location.

Xerocomus as a Mycorrhizal Fungus

Slipp and Snell (1944) have identified many species of Boletaceae that may form mycorrhizae with ponderosa pine and other western conifers. Examinations of natural stands of ponderosa pine in mixture with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in the Cascade Range of Oregon showed numerous so-called terrestrial toadstools. One of the most commonly occurring boletes has been tentatively identified as *Xerocomus* sp.[2] Cultural isolations were attempted from the sporophore caps, hymenium, and stipes of several collections, but without success. Therefore, a simple inoculation technique was employed to determine if this species of *Xerocomus* forms mycorrhizae with ponderosa pine.

Nine 6-inch flower pots filled with fine sandy loam (pH 6.4) were steam sterilized. After the pots were cooled, each was sown with 25 washed seeds of ponderosa pine. Eight months later the soil in 6 of the pots was inoculated with *Xerocomus* sp. Four 2-inch-deep holes were punched into the soil with a ¼-inch sterilized chisel, and one-fourth of each hole was filled with chopped tissue of fresh *Xerocomus* sp. sporophore caps. The holes were then filled with sterilized soil. Three pots were left uninoculated. All pots were placed in saucers indoors on window sills, and the soil was kept moist with tapwater placed in the saucers.

All together, there were 18 seedlings in the uninoculated pots and 21 seedlings in the inoculated series. At the time of inoculation the seedlings averaged about 2½ inches in height.

Four months after inoculation with *Xerocomus* sp. (seedlings approximately 1 year old), the roots of the plants were examined for mycorrhizae. Soil was carefully washed from the roots to prevent loss of root tips. Roots of the seedlings in the *Xerocomus*-inoculated series showed good development of ectotrophic mycorrhizae, while those in uninoculated soil showed no mycorrhizae. Moreover, the seedlings in the inoculated soil were somewhat taller and greener than those in the uninoculated pots.

This test, while not conclusive or conforming to pure cultural standards, strongly indicates that the *Xerocomus* sp. tested forms mycorrhizae naturally with ponderosa pine.

Discussion

Noxious sprays and gases are frequently used in forest nurseries to control damping-off, root rot, nematodes, insect infestations, and weeds. While effective control may result from such practices, undesirable effects on soil microflora are probable. Under certain conditions mycorrhizal fungi in the nursery soil will be affected unfavorably.

If seedlings are large enough as 1-0 stock for use in reforestation projects, the lack of mycorrhizae will probably not result in excessive mortality the first year, except under drought conditions. Generally, mycorrhizae will be acquired from the habitat in the second year to afford the seedlings a normal chance of survival. However, similar stock used in afforestation may give unsatisfactory survival after the first year, since mycorrhizae often are not present in the soil.

The use of injurious sprays or gases in the nursery may also result in stunted stock. In such instances the restricted growth of the seedlings may be due to retarded development of mycorrhizae on the plant roots. If this 1-0 stock is transplanted to untreated soil in the nursery, it probably will acquire mycorrhizae and reach plantable size as 1-1 seedlings for field use. Transplanting will, of course, temporarily interfere with nursery production, raise the cost of the stock, and limit the planting program. The quality of the stock, how-

[2]Personal communication dated October 2, 1953, from Prof. A. W. Slipp, College of Forestry, University of Idaho, Moscow, Idaho.

ever, can be more important than the quantity, and good development of mycorrhizae will definitely improve the quality of such species as ponderosa pine.

Summary

Chloropicrin and other poisonous gases used as soil fumigants in a ponderosa pine nursery destroyed the mycorrhizal fungi. At the end of the second year in the seedbeds, the nursery stock was stunted and chlorotic due to lack of mycorrihizae.

In 3 field trials of 800 seedlings planted on burned-over areas in 1951, stunted 2-0 nonmycorrhizal stock showed significantly poorer survival than normal-sized 2-0 stock with mycorrhizae at the end of the first growing season. Difference in size of stock, however, may have influenced survival somewhat. Losses during the second year after planting were not as high as during the first year, largely because seedlings originally without mycorrhizae had acquired the symbiont from the soil after transplanting.

Field plantations of 1,000 equal-sized, 2-0, nonmycorrhizal and mycorrhizal seedlings planted on a good site in 1952 showed significantly poorer survival at the end of the first growing season for the nonmycorrhizal stock. On 1,000 seedlings on a bunchgrass site, there was no significant difference, probably due to vegetative competition.

By a simple inoculation technique, it was found that *Xerocomus* sp., a bolete, formed mycorrhizae on the roots of ponderosa pine seedlings.

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Specific Gravity Indices for use in Breeding Loblolly Pine

BY
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IN A PREVIOUS STUDY (Zobel & Rhodes, 1956),[1] very high correlations were found between the specific gravity of the wood of a tree when young and the specific gravity of the same tree when mature. High correlations were also found between specific gravity of the bolewood and the specific gravity of limb sections, both terminal and adjacent. In the study cited above, the latter relationship was incompletely investigated, having been done only for trees with less than 8 rings in the bole crossection and for trees growing on only one site.

The present study concerns the efficacy of these limb sections for estimating stem specific gravity of trees with less than 8 rings, as well as those with a somewhat greater number, on several sites and with different growth rates. It gives indications of the apparent relationship between specific gravity of parent tree bole and that of the bole of its progeny as well as the relationship between the specific gravity of the bole of a young tree and that of its limbs. Relationships were significant, though test material was limited. Thus far in the study, no relationship has been found between the specific gravities of the boles of scion parents and the specific gravity of the limbs developed by grafted scions.

The studies reported are part of a project to develop a technique for evaluating young trees in progeny tests of high- and low-specific gravity trees without sacrificing the progeny. Such techniques will enable assessment of breeding results and selections at an early age and will reduce the long period of time now required to analyze results.

The senior author is Associate Professor of Forest Genetics at North Carolina State College, Raleigh, N. C. He was formerly Silviculturist, Texas Forest Service, College Station, Tex. The junior author is Associate Forestry Educator in the latter agency. The authors wish to express their appreciation to Mr. C. B. Godbey, Head of Genetics Department, Texas A & M College, for his assistance in the statistical analysis of the results of this study, and for his over-all suggestions and help. Also greatly appreciated was the review and many suggestions by Mr. Philip C. Wakeley, Southern Forest Experiment Station, New Orleans, La., who helped in the reduction of a mass of data to a relatively short, summary presentation.

[1]Zobel, Bruce and Robert Rhodes, 1956. Specific gravity estimations of mature loblolly pine from juvenile wood and seedling limb sections. For. Sci. 2:107-112.

Relationship of Specific Gravity of Limb to Bole

The relationship of specific gravity of limb to bole was determined by the following procedures. (See Zobel and Rhodes, 1956 for details). A 6-inch limb section was cut near the bole of the tree to be sampled, as near breast height as possible. This section is termed the adjacent section (Figure 1). Another 6-inch section was obtained at the end of the limb, below the current or growing tip. This is called the terminal limb section. A 6-inch section of the bole of the tree from which the limb arose was also obtained; this is referred to as the bole section. A departure from this procedure was necessary for the larger trees simply because no limbs were available at breast height. In this case the lowest limb available was used and compared with the bole section taken at breast height.

FIGURE 1. *Sampling of progeny of high and low specific gravity trees. Specific gravity was determined for the severed limb section to the left of the tree and for the bole section where it was attached. The limb section indicated is termed "adjacent."*

Specific gravity was determined by the standard method of relating green volume to dry weight. For the varied shapes of limbs and bole sections, green volume was determined by water displacement.

The previous study reported results for trees 3, 6, and 9 feet in height (Table 1, samples 1, 3, and 4). These trees were all from the same site. The present study included trees 4.5 feet tall taken from a different site (Table 1, sample 2), and trees 12, and 18 feet tall, from upland and flatland sites respectively. (Table 1. samples 5 and 8). In addition, the trees from the combined flatland and upland sites having less than 10 rings were combined (Table 1, sample 6). All the trees on the flatland and upland sites were combined for sample 7, Table 1. Approximately 30 trees were sampled on each site. Figure 2 shows graphically the relationship of bole to specific gravity of the limb section.

For all tests where terminal limb sections could be obtained (limbs on the 3-foot and 4.5-foot trees were too small), there was in each group either a highly significant or a significant correlation between limb and bole specific gravities (Table 1). For the younger trees highly significant results were obtained when adjacent limb sections were compared to the bole sections. A correlation analysis was run between terminal and adjacent limb sections, yielding $r = 0.7$. From this, and from the results in Table 1 it would appear that for small trees the adjacent limb section is satisfactory but that best results on the older trees may be obtained by using terminal limb sections.

Some other results of interest may be noted from Table 1. The specific gravity of bole wood increased up to about age 11, as would be expected. There was very little difference between the trees of the same

TABLE 1. Results of Correlation Analysis Between the Specific Gravity of Bole Wood and the Specific Gravity of Limb Wood.

Sample No.	Ave. tree ht. (Approx.) in Feet	Ave. age of bole section in years	Site	No. of trees	Sp. Gr. of bole	Limb Section	
						Adjacent[1] (r)	Terminal[1] (r)
1	3	2.5	Flatland[2]	30	.368	.772**	—
2	4.5	3.0	Dry, Deep Sand[3]	24	.358	.584**	—
3	6	3.3	Flatland[2]	30	.364	.692**	.596**
4	9	3.9	Flatland[2]	30	.384	.554**	.537**
5	12	10.2	Upland[4]	30	.486	.328	.381*
6	15	9.0	Upland and Flatland Comb.[5]	27	.479	.357	.487**
7	15	10.5	Upland and Flatland Comb.[6]	60	.483	.389**	.494**
8	18	10.8	Flatland[2]	30	.479	.444*	.591**

[1]r = coefficient of correlation. One asterisk indicates significance at the 5 per cent level and two asterisks significance at the 1 per cent level. Adjacent limb sections taken near the bole, terminal taken toward the end of the limb.

[2]Normally considered a good loblolly pine site. Shallow topsoil, heavy gray sub-soil, poor surface and sub-drainage.

[3]Upland site, deep sand, very rapid sub-drainage.

[4]An adverse upland site for loblolly pine. Topsoil removed and upper layers of red clay sub-soil removed for brick-making. Rapid surface drainage, slow sub-drainage.

[5]Sample 6 consists of those trees from the combined upland and flatland site that were 9 years of age.

[6]Combined data for the upland and flatland sites.

age on different sites. The relationship of specific gravity of the limb to bole sections was present on all sites studied. In summary, it would appear that the estimation of the bole specific gravity of a tree is feasible from its limb specific gravity, at least if it is under 11 years of age.

Inheritance of Wood of Varying Specific Gravity

A number of tests are under way to determine, under controlled conditions, the extent to which wood of varying specific gravity is inherited. A few preliminary results have been obtained, for small numbers of samples, which will be reported here. Although these results are from tests made on a small scale, results were all analyzed statistically.

Open pollinated seed were collected from two trees, one of high specific gravity (bole specific gravity at BH = .647), the other a low specific gravity tree (bole specific gravity at BH = .452). Seed from these trees were planted in the nursery in 1953, and the resulting seedlings out-planted the following year. Plantings were made at two locations: the Texas Forest Service's Temple Research Area, Fastrill, Texas and the A. J. Hodges Research Area, Many, Louisiana. Both were in deep sand, but the trees at Many were watered while those at Fastrill were not watered. Wood samples were taken while the progeny were in their third growing season. Thirty-six progeny of the high specific gravity tree and nineteen of the low specific gravity tree were analyzed. The analysis showed that both

limb and bole sections from the progeny of the parent tree with the high specific gravity were significantly higher than those from the parent tree with low specific gravity. (The results were significant at the 1 percent level.) This was true for adjacent and for terminal limb sections, and for both locations. However, no significant differences could be found between the Louisiana or Texas locations, or between the terminal or adjacent limb sections.

An analysis was also made of the inheritance of specific gravity of progeny from selfed loblolly pine parents. Three isolated trees with a number of 12-year-old progeny were located. Each group of trees was from one to several miles from the nearest loblolly pine capable of producing pollen, so pollination is presumed to be by selfing.

The parent with the highest specific gravity produced progeny with highest specific gravities (Table 2). One interesting point here is that the progeny of all three trees (*O*, *R*, and *U*) were the same age, yet those of tree *O*, growing much faster than the others, on a better site, had the highest specific gravities. This is counter

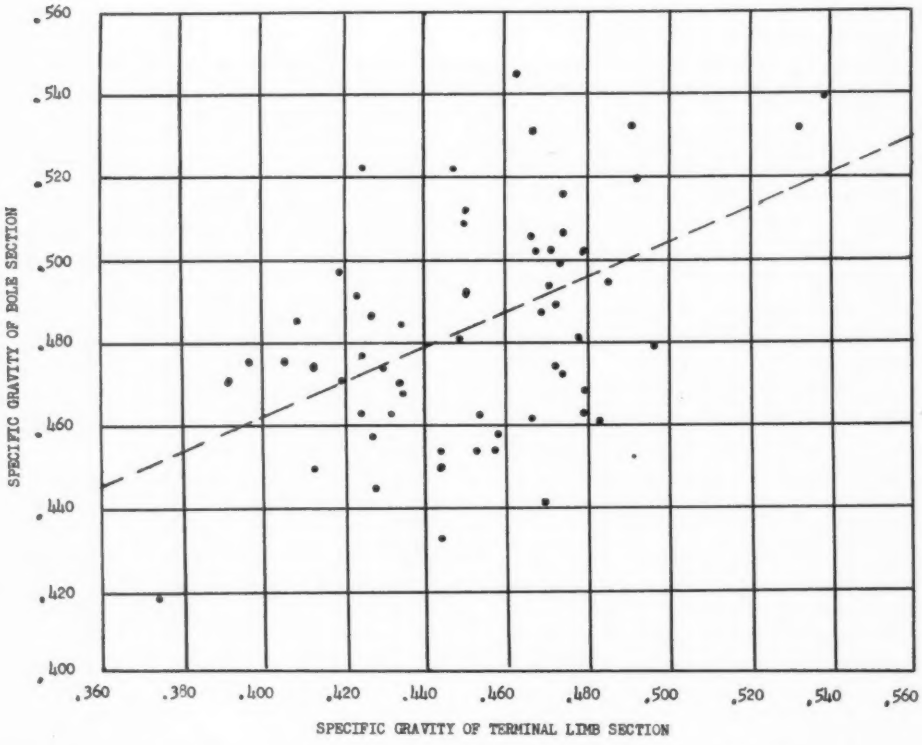

FIGURE 2. *Relationship of Bole Specific Gravity to Terminal Limb Specific Gravity for the Fifteen-Foot Group.*

TABLE 2. Specific Gravity of Parents and Progeny

Polination	Specific gravity		Progeny		
	Parent	Progeny	No.	Age	D.B.H.
Open pollination parent	.647	.358	36	4 years	—
	.452	.332	19	4 years	—
Selfed parents					
Tree *O*	.529	.497	25	12 years	7.5
Tree *R*	.507	.478	15	12 years	5.8
Tree *U*	.503	.460	21	12 years	4.9

to the claim[2] often made that high growth rate results in low specific gravity of the wood.

One further test of inheritance of specific gravity was made. Limbs were taken from 80 four-year-old grafts, twenty limbs from each of three clones which were grafts from parents with low specific gravity wood, and 20 limbs from the fourth clone which was from a parent with high specific gravity wood. For the four clones analyzed, no significant differences were found between specific gravities of the limbs of the grafts.

Summary

1. The use of limbs to estimate the bole specific gravity of trees up to 11 years of age is feasible; highly significant correlations were found between specific gravity of the bole and the limb sections. For all trees, either an adjacent or terminal limb section may be used, although the terminal sections tend to give better results on older seedlings. Specific gravity of terminal and adjacent limb sections were found to be highly correlated.

2. The limb-bole relationship enables an assessment of progeny tests at an early age by using limb sections which do not destroy the seedling. This was determined and checked for 4-year-old, open-pollinated progeny from two parent trees, one of high specific gravity and one of low specific gravity. The progeny of the high specific gravity parent had significantly higher wood specific gravity than that of the low specific gravity parent, both as indicated by limb section and by bole measurements.

3. Progeny of three supposedly selfed parents were analyzed. The progeny of the higher specific gravity parent had significantly higher specific gravity than the progeny of the lower specific gravity parents.

4. No correlation could be found between the specific gravity of the limbs of 4-year-old grafts and the specific gravity of the tree from which the grafts had been obtained.

5. Results reported here suggest an hereditary basis for wood density as expressed by specific gravity. These results are based on too few samples to be conclusive and more complete answers must wait until trees now growing in well-designed experiments are of an age and size suitable for analysis. However, in the five cases reported (two open-pollinated and three supposedly selfed) progeny from the higher specific gravity parents produced wood of higher specific gravity than did those progeny from the lower specific gravity parents.

[2]There are many references that could be cited in substantiation. The following two may suffice.

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Radial Growth in Forest Trees and Effects of Insect Defoliation

BY
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IT IS WELL RECOGNIZED that radial growth in forest trees is influenced by many factors, including climatic fluctuations, site, variable stand conditions, and defoliation. Severe or prolonged insect defoliation may cause modifications of the normal ring pattern that are useful in assessing the risk of imminent mortality and the need for control action. If old surviving trees are available, the modified ring patterns may be used in the reconstruction of outbreak histories many decades after the event (Swaine and Craighead, 1924; Blais, 1954). Critical cross-dating techniques are available for assigning year dates to ring sequences from dead trees (Ghent, 1952).

The most common source of radial growth data is a core, or disc, taken low in the stem, usually at breast height. The sequence of annual rings reflects the influence of many factors during the life of the tree, and as will be noted below, not all of them are extrinsic. Even the effects of severe and prolonged defoliation cannot always be segregated clearly from the effects of other factors, if one is dependent solely on cores or discs at breast height. Growth data from other sources are helpful: e.g. (a) higher levels in the same trees, for comparison with breast height records; (b) trees of the same species in nearby areas, known to have been free from infestation during the period in question; (c) trees of other species growing in the same stand, known to be unsusceptible or only moderately susceptible to attack by the insect defoliator. Visual comparison of the growth curves resulting from these various sources may be sufficient to clarify the influence of defoliation on growth of the susceptible species (Reeks and Barter, 1951).

In an attempt to eliminate the influence of climatic fluctuations, a crude method has been used in some unpublished Canadian studies of the effects of insect defoliation. The method is dependent on growth data for a companion species not attacked by the insect. It consists in converting the growth data for the susceptible species to a series of ratios, using the corresponding yearly records for the unsusceptible species as the appropriate divisors. This simple method assumes that the two species respond similarly to environmental factors other than defoliation, and that a decline in the series of ratios is a measure of the influence of defoliation alone. These are perhaps unwarranted assumptions even for tree species growing together—in fact, in-

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teractions might well be expected. The method has not been evaluated critically, and is unlikely to be used extensively now that more sensitive methods are available.

A voluminous literature has accumulated on tree ring analysis, but reference will be made here only to a few studies that throw light on the distribution of radial increment in tree stems. Onaka (1950) reviewed the literature on the vertical distribution of radial growth, and carried out numerous observations and experiments with *Pinus densiflora* S. and Z., *Pinus thunbergii* Parl., and *Chamaecyparis obtusa* S. and Z. He reported increase in ring width from the apex to the position of maximum branch development, and decrease in the lower part of the live crown. In the branchless portion of the stem, the distribution of ring width was related to tree condition: (a) in vigorous trees with large crowns, and in open-grown trees with large crowns and short branchless stems, ring width showed little or no decrease below the crown and often increased near the roots; (b) in close-grown trees with small to medium crowns, ring width decreased to a minimum near the base of the tree, and tended to increase abruptly at the root level.

From a series of disbudding, pruning, and girdling experiments, supplemented by measurement of growth hormone in the stem, Onaka concluded that the vertical distribution of radial increment is governed by the production and distribution of growth hormone and the flow of nutritive substances; that the growth hormone is produced by growing buds, cones, new and even old needles; and that nutritive substances are manufactured chiefly by old needles in the early part of the season and by new needles later in the season.

In a mathematical analysis of periodic cross-sectional growth in loblolly pine trees subjected to differential pruning, Labyak and Schumacher (1954) show that area increment is maximum at the base of the live crown; and that the contribution of branches in the upper crown, especially in the top one-tenth of tree height, is greatest at or near the base of the branch. The contribution of branches in the lower half of the tree is more or less evenly distributed over the stem between branch base and point of root influence.

The distribution of radial increment in red pine, *Pinus resinosa* Ait., has been studied systematically by Duff and Nolan (1953). From trees 15 to 30 years of age, complete records were taken of internodal lengths and the width of all annual rings in all internodes. The assemblage of ring measurements from a single tree, when plotted (see their Fig. 5), reveals an orderly design of ring widths which can best be described in terms of three sequences as follows:

Type 1 sequence. This is the series of measurements of the width of a given ring in all the internodes in which it occurs. The most recently formed ring has normally the longest series of measurements, comprising widths for all internodes from the apex of the tree to its base. The series of ring widths, starting at the apex, rises to a maximum in the first few internodes, and then gradually declines in successive internodes toward the base. This regular pattern, repeated by successive rings as they are laid down, is attributed by Duff and Nolan to nutritional gradients in the axis, arising from the distribution of foliage and incidence of light. Random extrinsic factors cause fluctuations in type 1 sequences, but these are usually masked by the characteristic "pattern" due to intrinsic growth factors.

Type 2 sequence. This is the series of width of rings laid down annually in any one internode, corresponding to conventional sequences based on a core or disc at breast height, or any other single level in the tree. The series of ring widths, starting at the center, typically rises to a maximum in the first few rings and gradually declines in successive rings toward the periphery. The strong pattern in the early

part of the sequence is derived from the pattern of the type 1 sequence and is therefore attributable to nutritional gradients. In the type 2 sequence, systematic variations in the pattern tend to obscure the effects of random extrinsic factors.

In the type 1 and type 2 sequences, the series of ring widths toward the base, or the periphery, are produced by progressively "older" cambia. At each successively lower internode in the type 1 sequence, the cambium producing the internodal section of the *same growth ring* is one year older than the cambium in the internode immediately above. Similarly, in any one internode, each successive growth ring is produced by cambium one year older than the cambium which produced the preceding growth ring. In any one internode, the *Xth* ring is therefore equally the *Xth* term of the appropriate type 1 and type 2 sequence.

Type 3 sequence. This is a unique sequence first defined by Duff and Nolan, from which the factors of cambial age and nutritional gradient are eliminated. The sequence consists of annual rings laid down by cambium of uniform age, but in successive internodes. The innermost ring in each internode from the apex downward would comprise such a sequence, based on radial increment of the year in which the leader of the tree was formed. The third ring in each internode from the third, downward, would comprise a sequence based on the product of cambium in its third growing season in each internode; and so on. The type 3 sequence is thus free from effects of nutritional gradient or cambial age, and is theoretically the best suited of the three types to portray the effects of extrinsic factors on radial growth.

Among extrinsic factors, Duff and Nolan recognize site quality and stand density, which have a systematic effect on radial growth, producing what is called "configuration" in type 3 sequences; and random variations, such as weather, which produce irregular fluctuations in the growth curve. To these, we would add a third category, neither entirely systematic nor random, but periodic and usually with cumulative effects for a period of years until the tree succumbs or recovers: we refer to serious defoliation that accompanies major outbreaks of defoliating insects.

The studies reported here had two objectives: 1) to determine whether patterns of radial growth similar to those in red pine are found in other species of comparable growth habit, as Duff and Nolan (p. 474) surmised would be the case; and 2) to determine the suitability of the various types of growth sequences as means of portraying the effects of insect defoliation on radial growth. These studies were extensions of work already in progress by the Forest Biology Division in stands of balsam fir, *Abies balsamea* (L.) Mill, var. *phanerolepis* Fern. in New Brunswick; of tamarack, *Larix laricina* (DuRoi) K. Koch, in Manitoba; and of lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelm. in Alberta. Balsam fir and lodgepole pine are comparable in general growth habit to red pine. However, balsam fir retains its old needles somewhat longer than red pine and lodgepole pine develops quite strong whorls of internodal branches. Tamarack differs from the other species in being deciduous; the nodal whorls of branches are less regular, and may be confused with internodal branches.

In referring to the several growth sequences in the following sections of this paper, we employ the following descriptive terminology; *oblique* sequence, equivalent to type 1 of Duff and Nolan; *horizontal* sequence, equivalent to type 2; and *vertical* sequence, equivalent to type 3.

We are indebted to our colleagues in the Forest Biology laboratories at Fredericton, Winnipeg, and Calgary for advice, criticism, and assistance during the investigations reported here; and to M. L. Prebble, Chief of the Forest Biology Division, for suggesting this co-ordinated study in widely separated parts of Canada, and for

editorial assistance in preparation of the manuscript.

Growth in Balsam Fir

Studies of radial growth of balsam fir were carried out by D. G. Mott in the Green River and Kedgwick watersheds in northwestern New Brunswick, in conjunction with long-term investigations of the ecology of the spruce budworm, *Choristoneura fumiferana* (Clem.).

Tree selection. For the investigation of growth sequences in balsam fir, trees were selected from two of the predominant age classes found in this part of the boreal forest region: immature stands of nearly pure balsam fir arising after the 1912-20 outbreak of the spruce budworm; and mature (80-year-old) stands of balsam fir with a small content of white spruce, *Picea glauca* (Moench) Voss. Both stand types are well stocked. White birch, *Betula papyrifera* Marsh., a minor component of these stands, was killed by "birch dieback" prior to the present outbreak of the spruce budworm. Since 1949, most of the susceptible stands of the spruce-fir association in northern New Brunswick have been subjected to repeated defoliation by the spruce budworm.

Tree A (Fig. 1) was a young, fully foliated balsam fir from the immature stand. It was representative of the codominant crown class, was 5.7 inches in diameter at breast height, and 43 feet in height. Tree B (Fig. 2) was a defoliated balsam fir, representative of the codominant crown class in the mature stand. It was 9.0 inches in diameter and 61 feet in height. Tree B died in 1954, following complete defoliation of the new growth each year from 1951 to 1954 and 65 percent defoliation in 1950.

In addition, less intensive growth measurements are presented for five trees from the immature undefoliated stand from which Tree A was taken, and on five trees from a comparable young stand which had experienced defoliation by the budworm from 1950 to 1954, to the extent of 20, 45, 91, 98, and 98 percent of the current new growth, respectively.

Growth measurement. Discs were taken from the midpoint of each internode, which could easily be identified by the whorls of branches, or the branch stubs or scars in trunk sections within or close to the crown. In lower parts of the trunk, frequent splitting was required to determine nodal points. Ring growth was measured to the nearest 0.13 mm. along two average radii in each disc, each ring width being thus the average of two measurements.

Growth sequences. The typical pattern of the *oblique* sequence is shown in four rings of tree A (Fig. 1a). This pattern occurs in balsam fir trees with crowns of moderate fullness, growing under conditions of moderate competition. Its gross features are the rapid increase of ring width to a maximum in the third to seventh internode from the apex of the tree, and the gradual decline of ring width in successively lower internodes. Deviations from the typical pattern are not uncommon. One of them is shown in Fig. 2a, where the 1945 ring of mature tree B maintained its width just short of the maximum in the 4th to the 25th internodes. Maintenance of ring width at the lower internodes was associated with well developed crowns and more exposed growing conditions in the mature stand.

Curves of the *horizontal* sequence for balsam fir (Figs. 1b, 2b) show the effect of the pattern of the oblique sequence, namely, increase in the width of successive rings at a given level in the tree to a maximum a few years after the internode is formed, and then gradual decline in rings laid down later in the same internode.

Curves of the *vertical* sequence (Figs. 1c, 2c) show no obvious pattern, but irregular fluctuations due to flowering, drought, and defoliation. The younger tree (Fig. 1c) had not yet produced heavy crops of flowers, but the older one had. The depressing effect of flower production on radial increment is clearly seen in the

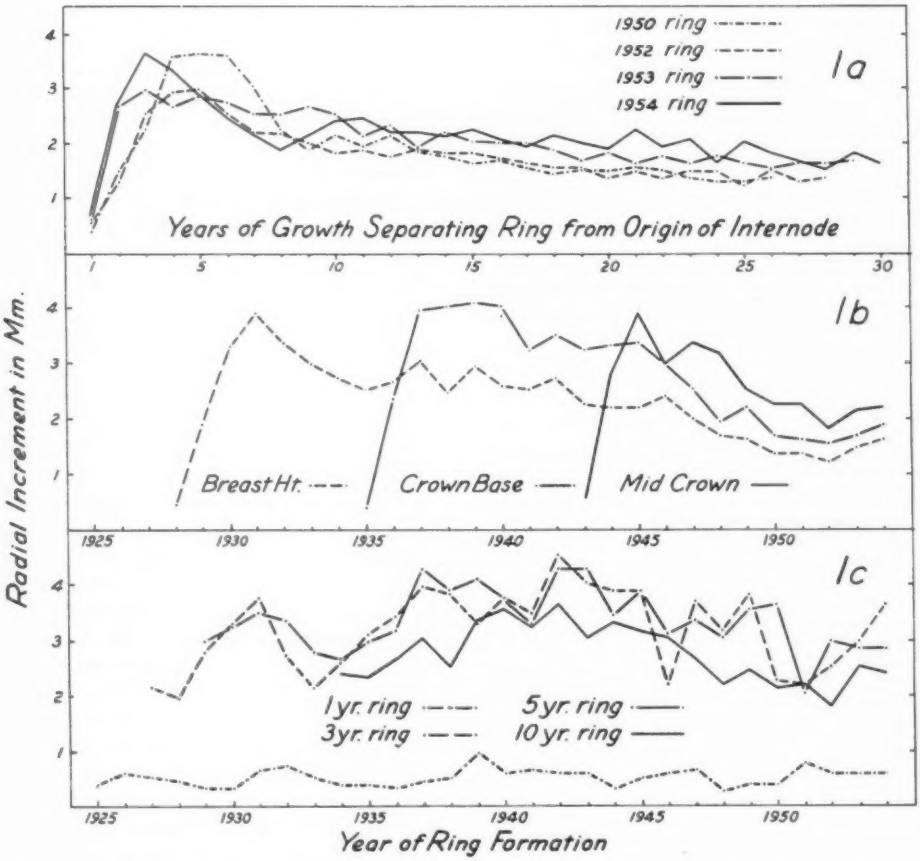

FIGURE 1. *Curves of radial growth in young, undefoliated balsam fir (tree A). Fig. 1a: curves of the oblique sequence for the 1950, 1952, 1953 and 1954 growth rings. Fig. 1b: curves of the horizontal sequence at the breast height, lower-crown and mid-crown levels. Fig. 1c: curves of the vertical sequence for the 1-, 3-, 5-, and 10-year rings. To show the pattern of the oblique sequence more clearly (Fig. 1a), all curves of this sequence have been aligned to a common scale on the X-axis, by using the abscissal scale "years of growth separating ring from origin of internode"—the ring formed in the year of internode formation being assigned number 1 in the series. If the internode numbers of the tree at time of felling had been used as the abscissal scale, the curves would be separated in the chart. The curve for the 1950 ring would start at the internode formed in 1950, the curve for the 1952 ring in the internode formed in 1952, and so on.*

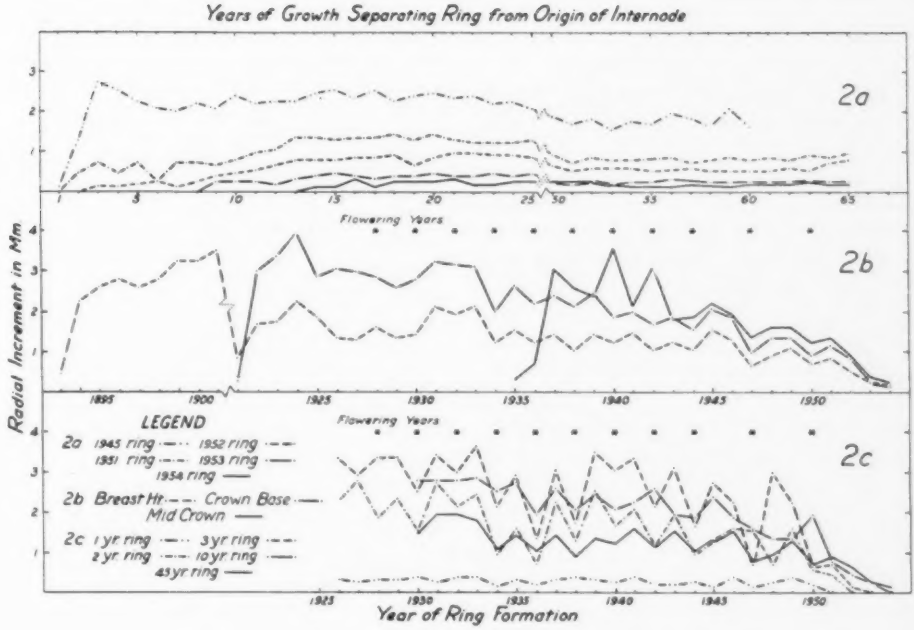

FIGURE 2. *Curves of radial growth in mature, defoliated balsam fir (tree B). Fig. 2a: curves of the oblique sequence for the 1945, 1951, 1952, 1953 and 1954 growth rings. Fig. 2b: curves of the horizontal sequence at the breast height, crown-base, and mid-crown levels. Fig. 2c: curves of the vertical sequence for the 1-, 2-, 3-, 10-, and 45-year rings. Years of staminate flower production are marked in Figs. 2b and 2c.*

curves of the vertical sequence (Fig. 2c), and to a somewhat lesser extent in the curves of the horizontal sequence (Fig. 2b). Morris (1951) has described several other effects of heavy flowering in balsam fir, including reduction of needle length and total foliage production.

Subnormal June rainfall, characteristic of northern New Brunswick from 1943 to 1948 (Greenbank, 1956), undoubtedly contributed to decline of growth in balsam fir stands at that time (Figs. 1c, 2c). However, the effect of drought was much less clearcut than that of frequent flowering and of defoliation after 1950.

Influence of budworm defoliation. Injury by this insect occurs in May and June. Mining of old needles and feeding on staminate flowers occur early in the spring before the vegetative buds have burst. Later, the larvae feed in the opening vegetative buds and destroy the newly-appearing foliage, and, when populations of the budworm are high, some of the older foliage as well. Damage is more severe in the tops of trees. The apex of the tree, the upper branches, and the tips of the lower branches begin to die after the third year of complete or almost complete defoliation of current foliage. Tree mortality

generally begins after the fifth year of severe defoliation (Belyea, 1952).

Seasonal and periodic increment of defoliated trees has been reported by Swaine and Craighead (1924), Belyea (1952), and Blais (1954), in the form of curves of the horizontal sequence, usually at breast height in the tree. Reduction of radial growth at breast height is first apparent one to three years after the first defoliation, and the growing period is progressively shortened by successive annual defoliations (Belyea, 1952). Effects of defoliation are seen in all three sequences of the mature tree (Fig. 2). Curves of the oblique sequence for the 1951 to 1954 rings (Fig. 2a) show a general reduction as contrasted with the pre-outbreak ring of 1945. Other effects of defoliation are lack of the characteristic maximum width in the upper internodes, and complete absence of the annual ring in the top of the tree for a progressively greater number of internodes as the defoliation continued in 1952 and later. In the year of death (1954), the current ring was very narrow from the 14th internode to the bottom of the stem, and was absent above the 14th internode.

Curves of the horizontal sequence (Fig. 2b) show great reduction of the 1952-54 rings laid down at the three levels. However, the influence of defoliation is confounded by the effects of flowering and the gradual decline of radial growth inherent in this type of sequence. The significance of growth reduction could be inferred if nearby stands of comparable age and density, free from budworm attack, were available for ring-growth studies. However, uninfested stands of susceptible age are uncommon during an active, widespread infestation. Since effects of budworm defoliation on ring growth are most severely and quickly reflected in the top of the tree, discs from the uppermost internodes should be included in series for careful study if accurate appraisal is to be expected from growth curves of the horizontal sequence.

Curves of the vertical sequence (Fig. 2c) reflect the effect of defoliation in various degrees. There was a general decline in all curves after 1950. The 45th ring declined gradually, but still had a measurable width in 1954 (this occurred in the 45th internode from the top of the tree). The 10th ring declined to zero in 1954, and the first- to third-ring sequence declined to zero in 1951, 1952, and 1953 respectively. These curves show the serious consequences of defoliation on ring growth in the upper internodes, but not so clearly as the curves of the oblique sequence (Fig. 2a).

Complete curves of the oblique sequence require measurements of each designated ring in each internode. However, since the pattern is essentially linear below the internodes of maximum ring width, an outline of the pattern may be obtained by measuring ring widths in each of the upper 10 or more internodes (to obtain the point of inflection), and thereafter at selected intervals, for example, every 10th or 15th internode. Oblique-type curves based on average ring measurements of five balsam fir trees, partially sampled in this manner and representing a young uninfested stand, are shown in Fig. 3a. All curves show the typical pattern of rapid rise in the upper internodes, gradual decline thereafter, and butt swell in the lowest part of the tree. Fig. 3b shows similarly abbreviated oblique-type curves for five trees from an infested stand. Progressive ring reduction occurred throughout the stem as the budworm defoliation continued from year to year. The consequences in this young stand were less drastic by 1954 than in the mature stand represented by Fig. 2.

Development of oblique-type curves based solely on measurement of selected internodes, will often be adequate to detect the effect of defoliation. The substantial saving of time arising from partial study of individual trees will permit more extensive sampling of stands, on the basis of tree size, crown class, defoliation history, and so on.

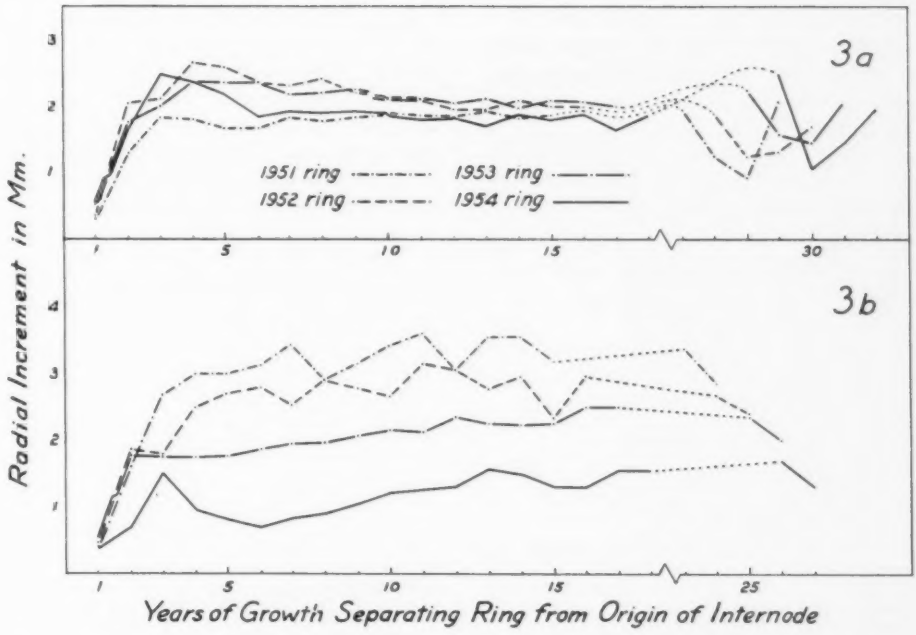

FIGURE 3. *Average curves of the oblique sequence for the 1951, 1952, 1953 and 1954 rings, based on partial sampling of the ring widths in 5 young, undefoliated balsam fir trees* (*Fig. 3a*) *and 5 young, defoliated trees* (*Fig. 3b*).

Growth in Tamarack

Radial and terminal growth of tamarack were studied by L. D. Nairn in Manitoba, as part of a series of investigations on the larch sawfly, *Pristiphora erichsonii* (Htg.).

Tree selection. For the investigation of growth sequences in tamarack, representative trees were selected from each of two tamarack stands in southeastern Manitoba, at the end of the 1953 growing season. These stands, as well as all others in the region, had been infested by the larch sawfly during recent years.

Tree C (Fig. 6) was 47 years old at the 1-foot level, was 5.1 inches in diameter at breast height, and 52 feet in height. It was representative of the dominant crown class of a dense, even-aged 50-year-old stand growing on a dry site near West Hawk Lake in the Whiteshell Forest Reserve. Tamarack, averaging 5 inches in diameter and 50 feet in height, comprised 90 percent of the stand; black spruce (*Picea mariana* (Mill.) B.S.P.), averaging 4 inches in diameter and 35 feet in height, made up the remaining 10 percent of the stand. Tree D was representative of the codominant crown class of a 30-year-old pure tamarack stand, and was situated at the edge of a small clearing in the stand. Both trees were given the same analytical treatment. Since the same results and conclusions are drawn from the two trees, curves are given here only for tree C.

Growth measurement. Radial and linear growth was recorded in every internode throughout the length of the stem. The upper four or five nodes were readily identified by the branch whorls, but difficulty was encountered in locating nodes in lower parts of the stem owing to the prominent development of internodal branches (Fig. 4). This problem was solved by locating the approximate position of the nodal points from the difference in ring counts in a series of discs along the stem. The stem was split in these regions and the nodes located by careful examination of the pith (Fig. 5). A disc was removed from every internode but its location was governed by the remaining unsplit portions of the internode. The annual rings were measured[1] and averaged for three radii on each disc. A complete record of the radial growth throughout the entire length of the stem was obtained and any desired sequence could readily be obtained from the data.

[1]Ring widths were originally measured to the nearest 0.01 inch. Rings of less than 0.01 inch were given a plus (+) rating but were valued at 0.005 inch in the calculations. In the interest of uniformity with other parts of this paper, the measurements have been converted to the metric system.

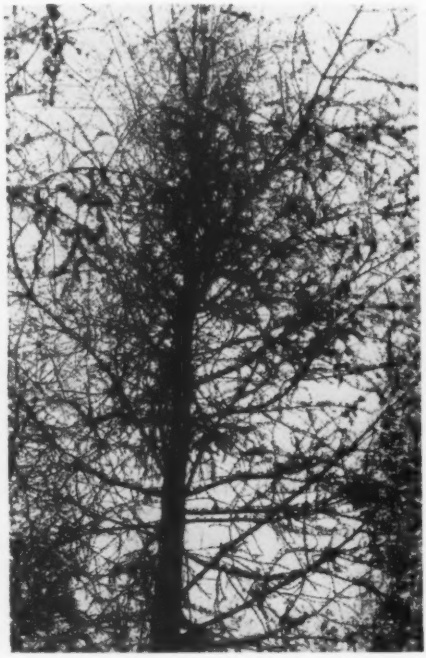

FIGURE 4. *Growth habit of tamarack, showing incomplete whorls of nodal branches and prominent development of internodal branches.*

FIGURE 5. *Nodal point in the pith of tamarack.*

Growth sequences. Typical *oblique* sequences are shown for the 1924, 1944, and 1947 rings in Fig. 6a. The width of each ring reaches a maximum at about the third or fourth internode, gradually declines in the following 10 to 20 internodes, and maintains a rather uniform low rate in the lower levels of the stem. Curves for the 1949, 1951, and 1953 rings are affected by sawfly defoliation and are referred to in a later section.

Horizontal sequences for the 1-, 16-, 33-, and 43-foot levels are shown in Fig. 6b. The curves for the upper three levels attain their maximum in the third to thirteenth rings from the pith, and then decline abruptly. The normal decline of the horizontal-type sequence is in this case greatly hastened by increasing competition within the stand, and by sawfly defoliation during the past five or six years of the growth record. The curve for the 1-foot level conforms with the others in the recent decline, and it also shows the typical pattern during the first five years. Its fluctuations during the intermediate period suggest

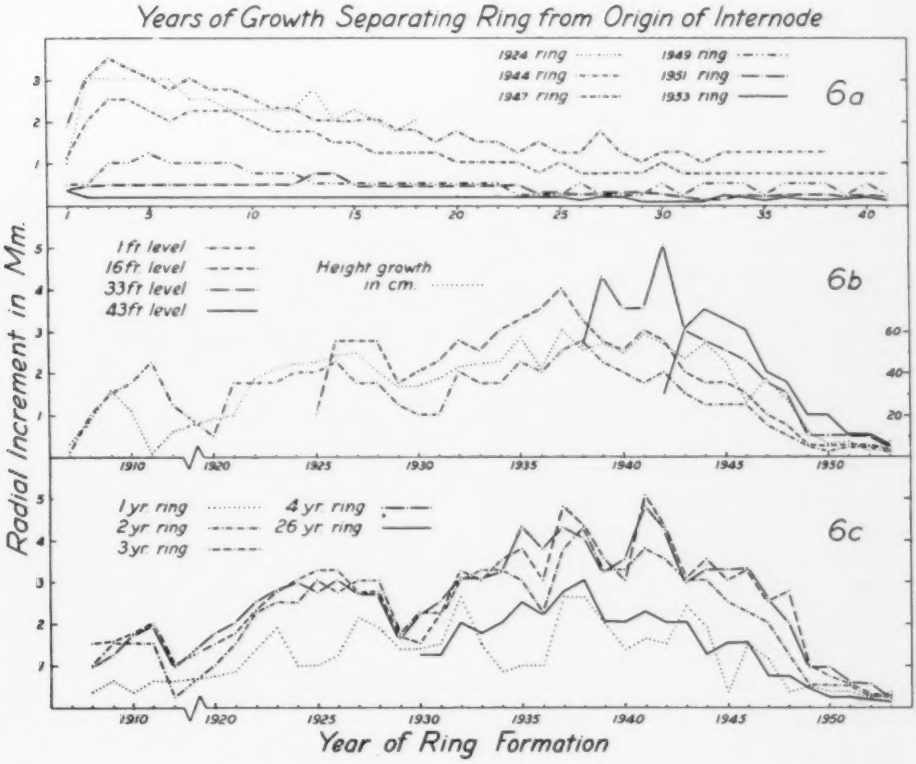

FIGURE 6. *Curves of radial growth in young tamarack (tree C). Fig. 6a: curves of the oblique sequence for the 1924, 1944, 1947, 1949, 1951, and 1953 growth rings. Fig. 6b: curves of the horizontal sequence at the 1-, 16-, 33-, and 43-foot levels. Height growth also shown, ordinate scale in cm. at right. Fig. 6c: curves of the vertical sequence for the 1-, 2-, 3-, 4-, and 26-year rings. Tree defoliated by the larch sawfly from 1947 to 1953.*

quite variable, but on the whole, good growing conditions until 1938.

Vertical sequences for the 1-, 2-, 3-, 4-, and 26-year rings are shown in Fig. 6c. The width of the 1-year ring, produced in each internode during the year of internode formation, is quite variable throughout the length of the internode, owing to taper of pith and xylem in the tree terminal. For reasons described earlier, it was not possible to make growth measurements in tamarack at the same relative points in different internodes, and this inconsistency in point of measurement casts doubt on the validity of the vertical sequence for the 1-year ring. This objection does not apply to sequences of rings laid down at a greater distance from the pith, because the effect of taper within the internode is largely absent after the year of internode formation.

Curves for the 2-, 3-, 4-, and 26-year rings are devoid of obvious pattern, yet show great consistency in their year-to-year fluctuations. These vertical sequence curves also vary consistently with the horizontal sequence curves for the same tree (Fig. 6b). Correlation between the vertical sequences and the horizontal sequence at the 1-foot level (which, among horizontal sequences, is least influenced by intrinsic growth pattern) is stronger for the vertical sequences based on rings at a greater distance from the pith (Table 1).

Annual height growth in Tree C (Fig. 6b) was measured as the distance between successive nodal points in the pith. A positive and significant correlation was found between annual height growth and radial growth as recorded in vertical sequences, as well as in the horizontal sequence at the 1-foot level in the stem (Table 2). Among the vertical sequences, that based on the ring nearest the pith was most strongly correlated with height growth, and there was a general decline in the degree of correlation as distance of the ring from the pith increased. The lowest correlation with height growth was shown by radial growth of the horizontal sequence. Duff and Nolan (1953) have shown that terminal growth is influenced by extrinsic as well as intrinsic factors. Among the former must be included factors that operate during the year of bud formation, and others that operate during the year of shoot elongation. On the basis of the correlation coefficients shown in Table 2 (similar results were obtained in tamarack tree D), from about 48 to 85 percent (r^2) of the variation in annual height growth of tree C may be

TABLE 1. Correlation between annual radial growth (horizontal sequence) at the one-foot level and various vertical sequences in Tamarack (tree C).

Vertical Sequences (based on indicated ring from pith)	n	r[1]
2	44	.790
4	44	.784
6	42	.681
9	39	.771
16	30	.867
26	22	.978

[1]All coefficients significant at 1 percent level.

TABLE 2. Correlation between annual height growth (internodal length) and radial growth as expressed in various sequences in tamarack.

Sequence Type	Ring No.	n	r[1]
Vertical	2	44	.921
"	4	44	.860
"	6	42	.822
"	9	39	.844
"	16	32	.888
"	26	22	.736
Horizontal (1-foot level)	2-47	44	.696

[1]All coefficients significant at 1 percent level.

attributed to variations in factors that caused concurrent fluctuations in radial growth.

Influence of sawfly defoliation. A recent outbreak of the larch sawfly affected most of the tamarack stands in western Canada after 1940. The larvae feed from the extremities of the branches inward and the peak period of feeding generally occurs in July. The needles are first consumed at the top of the trees and at the periphery of the crown. Complete defoliation is common in severe infestations. Annual radial growth of tamarack is almost complete in Manitoba before seasonal defoliation is at its peak. The effect of defoliation on radial increment is not apparent during the first year of an infestation. Severe defoliation of a healthy tree is followed by refoliation later in the same summer. Defoliation in successive years causes reduced production of foliage and shoots, death of lower branches and scattered tips, and ultimately the death of upper branches and, occasionally, the entire tree.

Defoliation was light from 1939 to 1946 in the tamarack stand in which tree C grew. Defoliation was recorded annually during the period 1947-1953, with results as follows:

Year	percent of defoliation	Year	percent of defoliation
1947	15	1951	45
1948	45	1952	90
1949	70	1953	75
1950	60		

The influence of defoliation may be seen in the several sequences of Fig. 6. Curves of the oblique sequence for 1949, 1951, and 1953 (Fig. 6a) show greatly reduced increment throughout the entire bole; in the last two of these there is complete obliteration of the characteristic maximum ring width near the top of the tree. Competition within the stand reduced radial increment whereas repeated defoliation by the larch sawfly eliminated the differential in growth rate normally reflected in greater ring width in the upper internodes. In oblique sequences for other years (not illustrated) there were inconsistencies in pattern, such as lack of a prominent maximum width in the upper internodes, or maintenance of uniform width in lower internodes. This suggests that such extrinsic factors as competition, drought, seed production, and defoliation affect the distribution of radial increment along the bole in different ways.

Curves of the horizontal sequence (Fig. 6b) reflect the influence of intrinsic factors causing pattern, extrinsic factors causing configuration, and random extrinsic factors. The effect of defoliation after 1947 cannot readily be separated from the effects of other factors which were operative as early as 1939 or 1940 (curves for 1- and 16-foot levels). Curves for successive ring widths at the 33- and 43-foot levels decline rapidly from their early maxima (1942 and 1944 respectively), the rate of decline being well established before larch sawfly defoliation became severe. The chief characteristic of the curves of the horizontal sequence during the later years is the minimal growth rate at all levels. The curves of this sequence do not permit identification of the year which first reflects the effects of defoliation, nor any clear evaluation of the extent of reduction due to defoliation in the later years.

Variation in curves of the vertical sequence (Fig. 6c) are, by definition, due exclusively to extrinsic factors. However, there is no clear distinction between the effects of competition, which was operative in the early 1940's, and of defoliation, which became severe six or seven years later.

This test of the three growth sequences in tamarack has been complicated by both the increasing competition in the stand and the absence of check trees free from sawfly defoliation during recent years. Under these handicaps, the horizontal and vertical sequences show the combined effect of competition and defoliation upon radial incre-

ment. Only the successive curves of the oblique sequence (Fig. 6a) show clearly a distinctive effect of severe defoliation, namely, elimination of the typical growth pattern of a given ring in the upper internodal sections of the stem.

Growth in Lodgepole Pine

Studies of radial growth of lodgepole pine were carried out by J. A. Cook as part of a series of investigations on the lodgepole needle miner, *Recurvaria starki.*, Free., in the region of Banff National Park, Alberta.

Tree selection. Two trees, among many studied, were selected for illustration of growth sequences in lodgepole pine. These trees were free from mechanical injury, frost or grazing damage, and abnormal competition, and were representative of the stands from which they were taken. Their crowns were well formed with distribution of the branches in regular whorls.

Tree E grew in a moderately dense, pure stand on a gently inclined slope near valley bottom in Kootenay National Park. The tree was 25 years old and 33 feet in height, with crown depth about two-thirds of tree height. So far as is known, there have been no insect infestations of sufficient intensity to cause defoliation during the life of young stands in this locality.

Tree F grew on the border of a mature, 100- to 110-year-old lodgepole pine stand on a 10 percent southwest slope in the Bow Valley near Lake Louise, in Banff National Park. The tree was 40 years old and 30 feet in height, with a well developed and regular crown. The area from which tree F was taken supported very heavy infestations of the lodgepole needle miner for several years.

Growth measurement. In lodgepole pine, there are commonly one or two, and occasionally three, internodal whorls of branches. Radial growth tends to be distorted in the immediate vicinity of the internodal branches, but this effect disappears about 1 to 1½ inches from the branch base. The pith has a moderate taper within a single internode, and the width of the first ring narrows quite strongly toward the apex. To avoid variability from these sources, ring measurements were made on discs taken one-third of the internodal length from the base. This point of measurement was always below the lowermost whorl of internodal branches. The average width of each ring was based on measurements in four radii of the disc.

Growth sequences. Representative *oblique* sequences for uninfested tree E are shown in Fig. 7a. The width of each growth ring increases to a maximum in the then third to sixth internode from the apex, and gradually decreases at lower points in the stem. Differences in the height of the various curves reflect the influence of external factors such as competition and weather. Reduced width of the 1954 ring, in comparison with those laid down earlier, is suggestive of increasing competition within the stand, but the evidence is not strong. Random seasonal variations in climate could equally be responsible for the observed differences in width of successive rings.

Fig. 7b shows *horizontal* sequences at the 4-, 6-, and 13-foot levels in tree E. At any one level, the maximum width is usually found in about the fifth ring from the pith. Secondary peaks in later rings (e.g., the 1947 and 1948 rings at the 6-foot level) during particular years, are indicative of sufficiently good growing conditions to override the typical pattern of the horizontal sequence.

The curves of the *vertical* sequence (Fig. 7c) illustrate the general trend referred to as "configuration." The trend for tree E is a gradual increase until about 1948 and a gradual decrease thereafter which probably resulted from increased stand competition. Sharper fluctuations which do not change the over-all trend

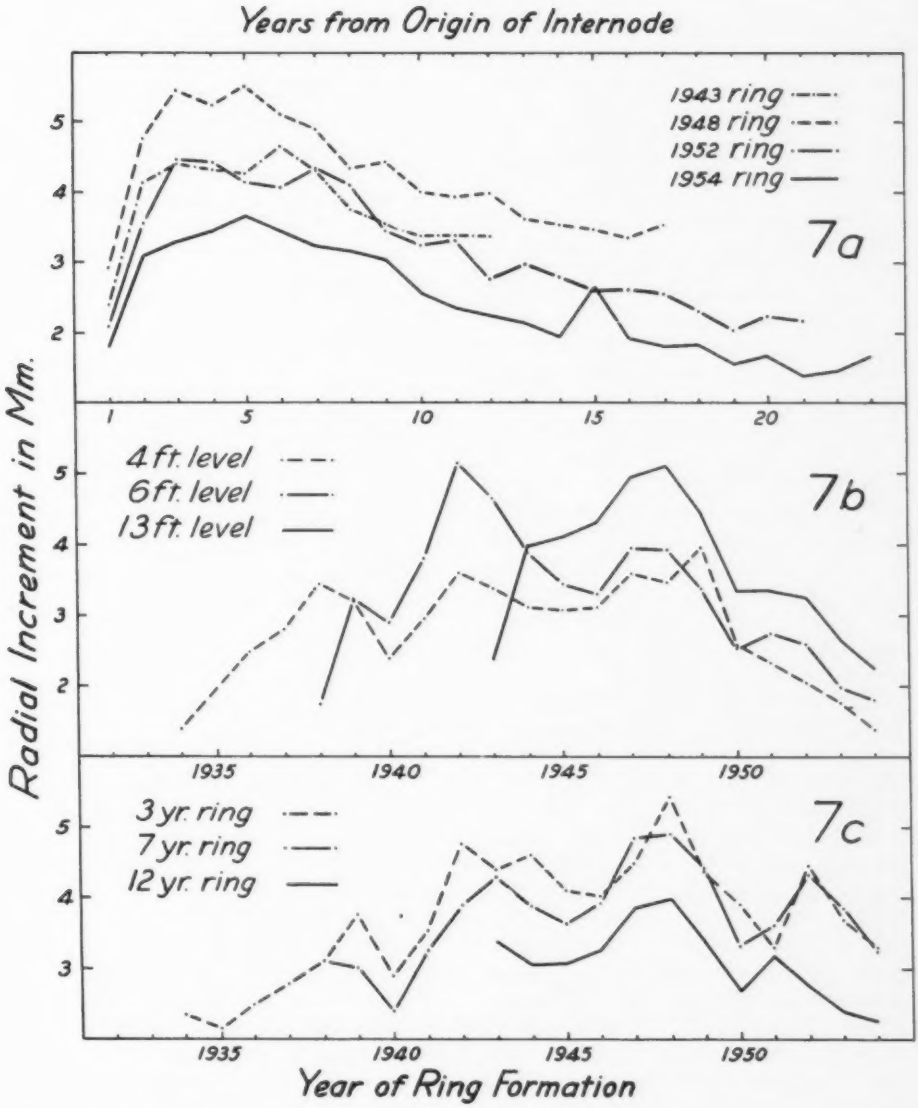

FIGURE 7. *Curves of radial growth in young undefoliated lodgepole pine (tree E). Fig. 7a: curves of the oblique sequence for the 1943, 1948, 1952 and 1954 growth rings. Fig. 7b: curves of the horizontal sequence at the 4-, 6-, and 13-foot levels. Fig. 7c: curves of the vertical sequence for the 3-, 7-, and 12-year rings.*

materially are probably the result of random weather factors.

Influence of needle miner defoliation. The lodgepole pine needle miner has a 2-year life cycle. Larval development extends over a 21-month period in three succeeding summers, and during this time each larva usually destroys three needles (Stark, 1954). The needle miner infestation is generally heaviest in the upper crown and in the younger needles. The gradual but cumulative loss of needles leads to reduced radial increment. Current studies indicate that defoliation of 40 to 50 percent is necessary to have a measurable effect on radial increment, and that the reduction of increment first appears about two years after defoliation (Stark and Cook, 1957).

The infestation was first noted in the Lake Louise area in 1942 (Hopping, 1946), but subsequent defoliation studies indicated that the infestation probably started in the 1930's (Stark and Cook, 1957). Owing to its size and position in the stand, tree F was possibly attacked some years later than the mature stand in the immediate vicinity. The infestation in this area declined after 1948, and was almost eliminated by severe climatic conditions in the winter of 1949-50 (Henson *et al.*, 1954). Since that time the needle-miner population has remained very low.

Figure 8 shows curves of the various sequences for tree F. Among the curves of the oblique sequence (Fig. 8a), that for 1938 precedes the infestation. The 1943 ring, formed in the early stages of the outbreak, lacks the typical maximum width in the upper internodes. The greatly depressed 1948 ring shows the full effect of progressive defoliation. Although the 1954 ring shows some improvement following the decline of the needle miner, the weakened condition of the upper crown is evident in the flattened growth curve for the topmost internodes. If curves for all rings were introduced into Fig. 8a, there would be a more gradual merging of the curves of the pre-infestation and the infestation periods, each curve being influenced by intrinsic as well as external factors. Even with the full complement of curves, some doubt remains as to the year in which the influence of defoliation was first reflected in the curve of ring growth.

Curves of the horizontal sequence for the 4-, 10-, and 16-foot levels (Fig. 8b) show the gross effects of defoliation, namely, several years of decline leading to minimal growth in the period 1947-1951, and slight recovery in 1952 to 1954 following reduction of the needle miner population. The first consistent and sustained reduction in the three curves occurred in 1943, and one might attribute this to the effects of defoliation in 1942, or earlier. However, from the evidence of horizontal sequence curves alone, this interpretation would be open to question: a similar decline might be initiated by growth pattern (see growth curves, 1949 to 1954, in undefoliated tree E, Fig. 7b), or confused with the effects of unfavorable growing conditions.

Curves of the vertical sequence for tree F (Fig. 8c) show an upward trend in the configuration until 1942, where there is a sharp break and a decided downward trend to a low point between 1946 and 1952. Later, the curves rise again. Only severe and prolonged defoliation by the lodgepole needle miner can account for the great depression of growth after 1942. If tree F had not suffered needle miner attack, it is reasonable to expect that the general growth trend would have been similar to that which prevailed before 1942, and to the growth trend in uninfested tree F after 1942. Therefore, 1943 can be accepted with reasonable assurance as the first year of radial increment reduction due to defoliation by the needle miner. If the configuration trend is properly evaluated, it is possible to define the first year of increment reduction due to defoliation as well as the period of severely depressed growth. Confusion due to the influence of random climatic fluctuations can be eliminated to a large extent by careful appraisal

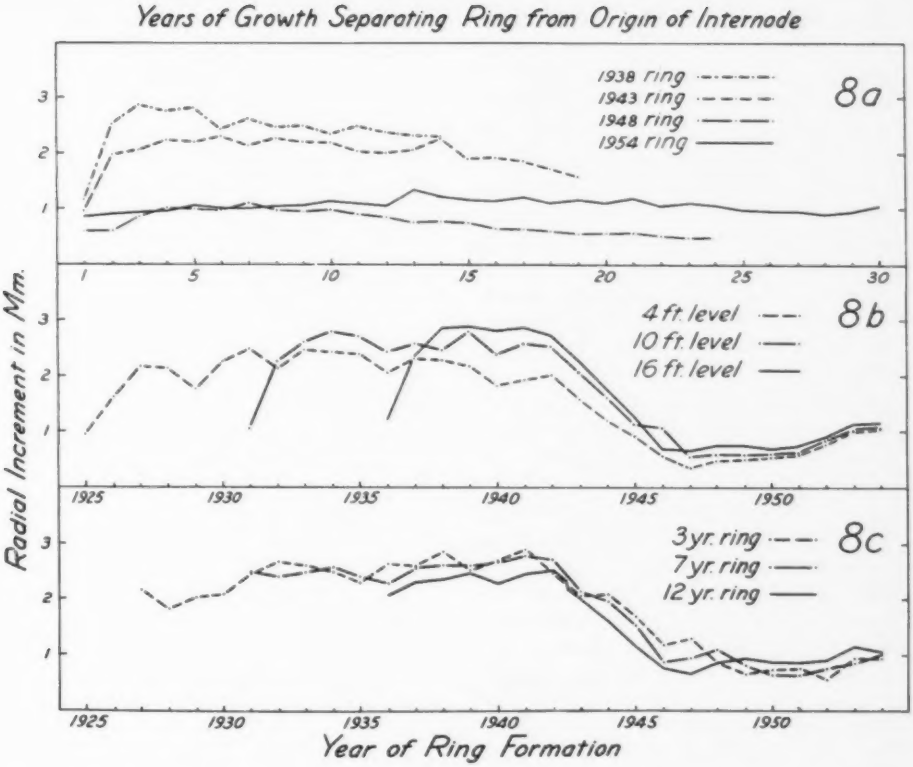

FIGURE 8. *Curves of radial growth in young, defoliated lodgepole pine (tree F). Fig. 8a: curves of the oblique sequence for the 1938, 1943, 1948 and 1954 growth rings. Fig. 8b: curves of the horizontal sequence at the 4-, 10-, and 16-foot levels. Fig. 8c: curves of the vertical sequence for the 3-, 7-, and 12-year rings.*

of the over-all trend in contrast with these minor departures.

Summary and Conclusions

These studies have shown that the distribution of radial growth in balsam fir, tamarack, and lodgepole pine trees growing in natural stands, follows the patterns described by Duff and Nolan (1953) for plantation-grown red pine. In the *oblique* sequence (Type 1 of Duff and Nolan), the width of a given ring, measured in the successive internodes throughout the length of the stem, rises to a maximum in the first few internodes below the apex of the tree, and then gradually declines in successively lower internodes. This pattern is repeated in successive rings as the tree grows in height and diameter.

In the *horizontal* sequence (Type 2 of Duff and Nolan), the width of successive annual rings from the pith to the periphery of the stem reaches a maximum among rings laid down very early at any given height in the tree, and then declines gradually throughout the remaining rings at that

level. This attribute of the horizontal sequence follows naturally from the inherent growth characteristics of the tree as expressed in the pattern of the oblique sequence. Typically, the number of the ring having maximum width in the horizontal sequence would correspond to the number of the internode having maximum ring width in the oblique sequence. The early portions of oblique and horizontal sequences are dominated by inherent growth patterns attributed by Duff and Nolan to the influence of nutritional gradients in the tree.

In the vertical sequence (Type 3 of Duff and Nolan), each year's radial growth is the width, in a given internode, of a ring produced by cambium of uniform age. For example, a vertical sequence based on the 3-year ring would be made up of the following terms: the outside ring in the 3rd internode from the top of the tree, for the current year; the 3rd ring in the 4th internode, for the current year less one; the 3rd ring in the 5th internode, for the current year less two; and so on. Similar sequences may be based on any given ring from the pith. The vertical sequence is thus free from the effects of nutritional gradients in the tree, and hence, from inherent pattern; and it may show more clearly than do the oblique and horizontal sequences the effects of certain extrinsic factors, such as climatic fluctuations, changing competition within the stand, defoliation, and incidence of heavy flowering. The influence of recurrent flowering on ring growth of balsam fir is shown in the vertical sequences of Fig. 2c.

The influence of insect defoliation on radial growth was of particular interest in this study. In balsam fir trees defoliated by the spruce budworm, the reduction of radial growth shows up in growth sequences of all three types (Fig. 2). The oblique sequences portray the extent of the progressive reduction throughout the entire stem. In the early years of severe defoliation, the characteristic maximum ring width in the upper internodes is suppressed; later, the ring in the upper part of the stem is completely obliterated for a progressively greater number of internodes. The horizontal sequences at mid-crown and lower crown levels show great reduction of the most recent rings, but effects of defoliation are confounded in part by inherent pattern and by other extrinsic factors such as flowering. The vertical sequences show great reduction of all rings and early obliteration of radial growth in the rings of youngest cambial age, as a result of budworm defoliation. This is consistent with conclusions drawn from the oblique sequences but is not so clearly portrayed, owing to the more involved make-up of the vertical sequence.

The ability of the three sequences to portray the earliest influence of defoliation on radial growth is also of interest. Defoliation of the new foliage of the balsam fir tree illustrated in Fig. 2 was about 65 percent in 1950, and 100 percent in each of the following four years. The oblique sequence shows a marked effect on radial increment in 1951; the horizontal sequence at mid-crown and lower levels, shows a possible effect on radial increment in 1952; and the vertical sequence shows elimination of the 1-year ring in 1951, and similar results for 2-, 3-, and 10-year rings in later years. Sequences of the oblique type appear to be the most useful in portraying the influence of budworm defoliation on radial increment in balsam fir.

In tamarack trees defoliated by the larch sawfly, reduction of radial growth is evident in curves of all three sequences (Fig. 6). The oblique sequences have advantages similar to those detected in the analysis of balsam fir defoliated by the spruce budworm. The horizontal sequences show great reduction at various levels in the stem, but the first evidence of reduction due to defoliation is confounded by pattern and fluctuations in extrinsic factors other than defoliation. The vertical sequences show the great sensitivity of the rings formed by

young cambium to fluctuations in extrinsic factors, but the effects of increasing competition and of defoliation are confused in the growth curves.

In lodgepole pine trees defoliated by the lodgepole pine needle miner (Fig. 8), oblique sequences give the best portrayal of growth reductions throughout the stem. However, in the trees studied there was a gradual decrease in the height of oblique-type curves throughout the outbreak period and it was not possible to detect which ring showed the first effects of needle-miner attack. Vertical sequences are superior to horizontal sequences as an indicator of the earliest year of ring reduction due to defoliation.

Growth sequences of the oblique type appear to have peculiar advantages in studying the effects of insect defoliators on radial growth of conifers, especially where injury is more severe in the tops of the trees. Conventional sequences of the horizontal type are less useful; for if taken at low levels in the stem where radial growth is approaching its characteristic minimum, growth fluctuations are less sensitive to environmental changes; and if taken at high levels in the stem, effects of defoliation are likely to be confused with effects of pattern. Sequences of the vertical type have a theoretical advantage over those of the other two types, owing to removal of the effects of pattern. Effects of defoliation and other extrinsic factors should be most clearly portrayed in sequences of rings laid down by "young" cambia, which produces rings of maximum width. In practice, if the object is not only to obtain a measurement of the effect of defoliation over a period of years, but also to detect the first year showing the effect, sequences of both the oblique and vertical types would be desirable. The same series of discs from the internodal points will supply the data for both types.

In preparing sequences of the oblique and vertical types, it is unnecessary to measure all ring widths in all internodes. In oblique sequences, the width of each ring to be studied should be measured in each of the upper 10 or more internodes to establish the growth curve above the point of typical maximum; but to establish the level and shape of the curve at lower points in the stem, ring measurements in every tenth or fifteenth internode should suffice. In vertical sequences, the longest series can be prepared for rings laid down by "young" cambia, i.e., the 1-, 2-, and 3-year sequences, and these are also most sensitive to changing environmental conditions. In preparing growth curves of the vertical sequence type, each year during the period of special interest should be represented by ring measurements in the appropriate internodes, but earlier or later periods could be represented by ring measurements in conveniently selected internodes. Further studies are being made of the usefulness of partial growth sequences in balsam fir, tamarack, and lodgepole pine.

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